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ANNALE VAN DIE
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BAND 84



ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 84 BAND



THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

DIE TRUSTEES VAN DIE
SUID-AFRIKAANSE MUSEUM
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1981

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FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.
KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.
KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
THEILE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

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PALAEOECOLOGY OF THE LATE
TERTIARY FOSSIL OCCURRENCES IN
'E' QUARRY, LANGEBAANWEG,
SOUTH AFRICA, AND A REINTERPRETATION
OF THEIR GEOLOGICAL CONTEXT

By

Q. B. HENDEY

Cape Town Kaapstad

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PALAEOECOLOGY OF THE LATE TERTIARY FOSSIL OCCURRENCES IN 'E' QUARRY, LANGEBAANWEG, SOUTH AFRICA, AND A REINTERPRETATION OF THEIR GEOLOGICAL CONTEXT

By

Q. B. HENDEY

South African Museum, Cape Town

(With 17 figures and 9 tables)

[MS. accepted 26 November 1980]

ABSTRACT

The late Tertiary succession in the vicinity of Langebaanweg, Cape Province, is correlated with the global sea-level changes of that period. The principal fossiliferous elements are the Quartzose Sand Member (QSM) and Pelletal Phosphorite Member (PPM) of the Varswater Formation, which were laid down during the global early Pliocene transgression. The nature of the succession was determined by the physical geography of the region, while the preservation of an unusually large body of early Pliocene sediment in the Langebaanweg area was due to the development at that time of an overlying coastal barrier complex, part of which survived subsequent erosion.

All elements in the succession are fossiliferous in parts. Approximately 230 invertebrate and vertebrate taxa are recorded from the Varswater Formation, in which a variety of marine, freshwater and terrestrial depositional environments are represented. Species assemblages, body part representation and condition of specimens vary according to the facies from which they are derived. The fossils reflect the changing environmental conditions of the late Miocene and early Pliocene, when local temperatures moderated from tropical to temperate, rainfall was changing from a summer to a winter maximum, and woodland vegetation was giving way to more open grasslands and fynbos.

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INTRODUCTION

General

Langebaanweg (18° 9'E, 32° 58'S) is situated in the south-western Cape Province approximately 110 km north-north-west of Cape town, and a little less than 2° north of the most southerly tip of Africa (Cape Agulhas) (Figs 1–2). It is about 13 km inland (north-east) from Saldanha Bay, and 21 km south of the mouth of the (Great) Berg River at St Helena Bay. The settlement originally consisted of little more than a railway siding, but during the Second World War the commencement of phosphate mining operations and the construction of a military airfield enlivened the area.

The phosphate deposits of the area have long been known, and although commercial exploitation commenced in 1943, it was not until 1958 that the occurrence of vertebrate fossils in these deposits was reported (Singer & Hooijer 1958). Since then the area has become one of the most prolific sources of late Tertiary fossils in Africa. Phosphate has been mined in two areas, and both have yielded fossils. Initially mining was confined to an area immediately west of the Langebaanweg railway station. This open-cast mine, known as Baard's Quarry, was relatively small, and although large quantities of fossils were recovered, most are unidentifiable fragments (Hendey 1978a). About 2 km further west is Varswater, a subdivision of the farm Langeberg, where mining also started on a small scale, with few fossils having been recovered. During 1965 a start was made on the New Varswater Mine ('E' Quarry), a comparatively large undertaking which has been the source of the vast majority of fossils from the Langebaanweg area (see Hendey 1970a, 1974a, 1976a, and other publications cited below).

This report deals largely with the fossils and deposits of that part of the 'E' Quarry sequence which comprises the late Miocene/early Pliocene Varswater Formation. In order that this element in the succession be placed in perspective, an account is also given of other late Tertiary deposits in the vicinity. The entire succession is correlated with others on the west coast of southern Africa, and to the record of global sea-level changes.

The emphasis in the palaeontological sections is on the palaeoecology of the Varswater Formation. 'Palaeoecology' was defined by Olson (1962: 134) as referring 'precisely to the ecology at some ancient time or times and thus, strictly, is an interpretation of the once living biological-physical system'. The primary requirement in any such study is the identification of the plants and animals which lived at the time in question. To this must be added a determina-

tion of the prevailing environment, that is, the physical setting and the climate. Only then can the relationships of the plant and animal communities to each other, and to their surroundings, be assessed.

Although comparatively little is known of the vegetation in Varswater Formation times, the geology and fauna of the deposits have already been

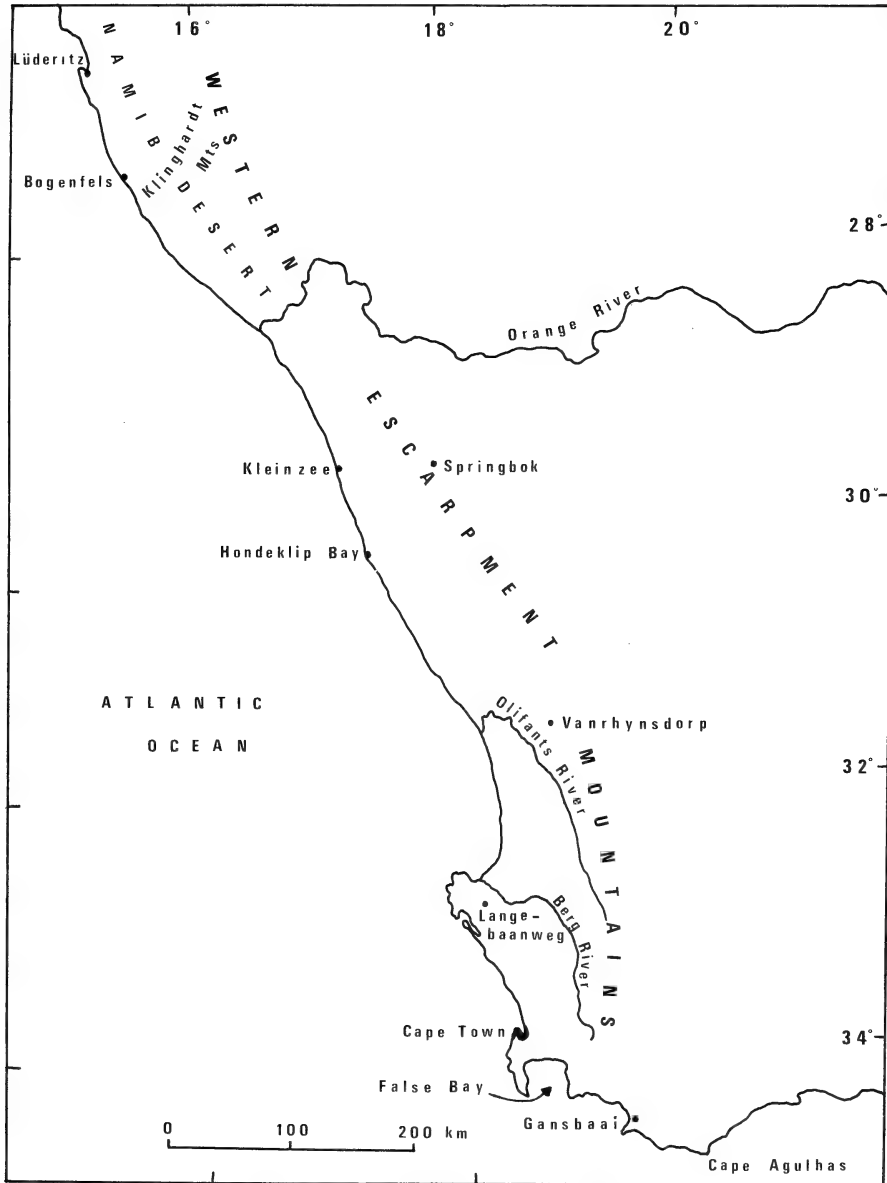


Fig. 1. The west coast of southern Africa.

studied in some detail. Previous publications resulting from these studies have included palaeoecological interpretations, and these are either simply referred to, or the information they contain is repeated here, usually in an abbreviated form. In addition, some previously unpublished observations are included. This synthesis is intended only as an interim report, since relevant research is continuing.

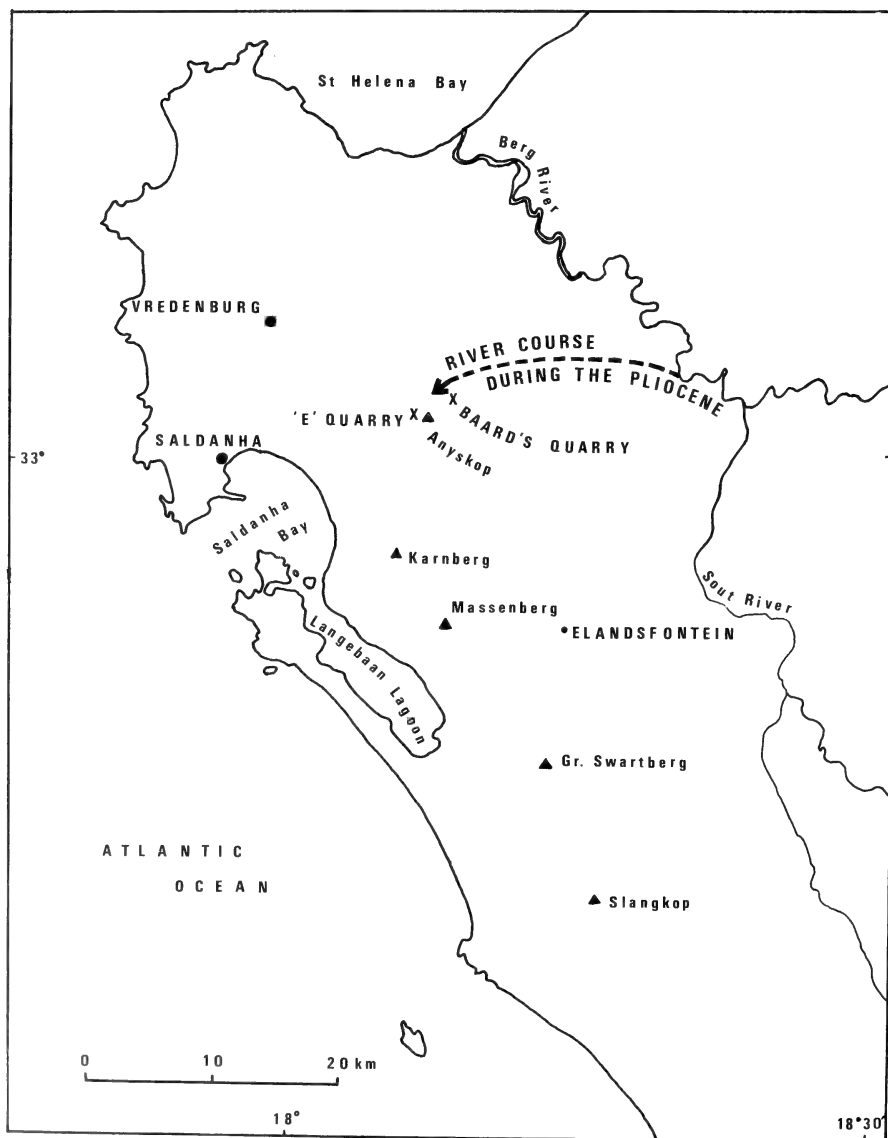


Fig. 2. The Saldanha region of the south-western Cape Province.

While the 'E' Quarry fossils and deposits have already provided a wealth of palaeoecological information, a great deal more is promised by further identification of taxa and detailed analyses of the nature and composition of fossil assemblages from particular horizons or areas. The combination of an unusually rich fauna, some palaeobotanical information, and a complex variety of depositional environments, dating from a period when significant environmental change was taking place, makes 'E' Quarry an excellent subject for palaeoecological studies.

Stemming from the accounts of the geology and biology of the 'E' Quarry deposits is a statement on some evolutionary aspects of the recorded fossil mammals, together with a reassessment of the age of the principal fossil occurrences in the area.

Present environment

The south-western Cape Province has a Mediterranean type of climate (Cs of Köppen), and Langebaanweg is situated in the more arid north-westerly part of this region. Rainfall is brought by the westerly wind system of southern mid-latitudes, which is usually far enough north to affect the area only during winter. Coastal fogs sometimes penetrate to the area during cooler months. The mean annual precipitation is about 250 mm. Winters tend to be cool rather than cold, and very rarely are sub-zero temperatures experienced, and then only at night. The summers are dominated by high-pressure systems in the south Atlantic and are long and dry. Although temperatures may be high (up to 40 °C), they are often moderated by the prevailing south-easterly winds. These winds are frequently moderate to strong, and, being dry, they aggravate the summer aridity by desiccating both the soil and plants. The low temperatures of the adjacent South Atlantic Ocean are caused by an upwelling of Southern Ocean water in the Benguela Current System. This cold water is a major factor contributing to the aridity of the region. A summary account of the climate of the south-western Cape and adjacent regions was given by Fuggle & Ashton (1979).

In the immediate vicinity of Langebaanweg there is no naturally occurring surface fresh water, except for small ephemeral ponds during winter. Otherwise surface fresh water is available locally only at isolated springs, such as that associated with the Quaternary fossil occurrences on the farm Elandsfontein, 20 km to the south-east (Hendey 1974a), or in the Berg River, 15 km to the north-east. The Berg River is perennial and is the largest river in the south-western Cape, draining the major part of this region (Harrison & Elsworth 1958; Harrison 1964).

The sclerophyllous natural vegetation, which has been considerably disturbed by human activity, is classified as 'coastal fynbos', which in this sandy area is 'predominantly ericoid and rather open, the bushes being somewhat rounded and up to 1 m high' (Taylor 1978: 204). Proteoids, restioids, grasses, geophytes, and annuals are present, but there are no indigenous trees. A

detailed account of the vegetation in the near-by area surrounding Langebaan was given by Boucher & Jarman (1977).

The fauna of the area has been depleted during historic times (post-seventeenth century). No larger mammals survive, although smaller ones are not uncommon. They include a variety of insectivores, bats and rodents (including a porcupine), a hare, small carnivores (genets, mongooses, a wildcat, foxes), and small antelope (steenbok, grysbok and probably grey duiker). Birds are both diverse and abundant, nearly 100 species having been recorded in or near 'E' Quarry (G. Benfield, pers. comm.). This is due largely to the artificially well-watered environment created by the open-cast mining, which has extended below the water-table in places. Lower vertebrates include frogs, tortoises, lizards, and snakes. Invertebrates are common and include the land snail, *Trigonephrus*, shells of which are frequently found in local terrestrial deposits of late Cenozoic age.

GEOLOGY

THE LANGEBAANWEG SUCCESSION

The Cenozoic deposits in the vicinity of Langebaanweg have been the subject of many published and unpublished studies, partly because of the economically important phosphate occurrences, and partly because they are in places so richly fossiliferous. At its maximum development the local succession comprises over 100 m of clastic sediments resting on a pre-Mesozoic bedrock. These deposits are largely unconsolidated, and the earliest evidently date back to the early or middle Miocene, followed by a substantial element dating from the Pliocene, while the succession is completed by a nearly ubiquitous covering of Quaternary sands.

The most recent account of this succession, and the only one that deals with it in its entirety, is that of Rogers (1980), whose lithostratigraphy (Table 1) is basically similar to that recognized in earlier studies (e.g. Hendey 1973, 1974a, 1976a, 1980; Tankard 1974a, 1975a, 1975b; Dingle *et al.* 1979). The earlier studies centred largely on the phosphate and fossiliferous deposits of the Varswater Formation (*sensu* Tankard 1974a), which are best known from the exposures in 'E' Quarry.

The 'E' Quarry succession was initially interpreted largely on palaeontological grounds (Hendey 1973, 1974a), and this was followed by detailed studies of the deposits themselves. Tankard's (1974a) definition, description and discussion of the Varswater Formation in 'E' Quarry and adjacent areas is the standard reference on the subject. In a subsequent study, Tankard (1975a) dealt with those deposits underlying the exposures in 'E' Quarry and included them in the 'Saldanha Formation'. He gave a useful review of all the information then available in an unpublished thesis (Tankard 1975b).

The 'E' Quarry succession has since been discussed by Hendey (1976a, 1980), Dingle *et al.* (1979), and Rogers (1980), while the latter two studies also take into account underlying and overlying deposits.

TABLE 1

The lithostratigraphy of Cenozoic deposits in the vicinity of Langebaanweg, Cape Province.

Rogers 1980		This Report	
Formations	Subdivisions	Subdivisions	Age
Bredasdorp	Langebaan Limestone Member (in part)	Surface sands (including duricrusts)	Pleistocene and Holocene
		Baard's Quarry fluvial deposits	Late Pliocene or early Pleistocene
Bredasdorp	Langebaan Limestone Member (in part)	Anyskop terrestrial deposits	Late Pliocene
		Anyskop marine deposits	
Varswater	'phosphorite member' (including beds 3aS and 3aN)	Pelletal Phosphorite Member (PPM) (including beds 3aS and 3aN)	Early Pliocene
	'quartzose sand member' (including 'peat bed' & 'clay bed')	Quartzose Sand Member (QSM) (including floodplain, peat & tidal flat beds)	
	'gravel member'	Gravel Member (GM)	Late Miocene
Saldanha		Pre-GM deposits	Middle Miocene
Elandsfontyn			

Changes in the nomenclature of the subdivisions of the Varswater Formation have been frequent enough to cause confusion, which is unfortunate since the lithostratigraphy recognized in the various studies has remained virtually unchanged (Rogers 1980, table 3.8). The most distinct of the recent terminologies is that of Dingle *et al.* (1979), and, although it is concise and comprehensive, the largely informal terminology used in all post-1975 palaeontological studies is retained here, with the addition of some completely informal terms which refer to pre- and post-Varswater Formation (*sensu stricto*) deposits.

The latter deposits have hitherto received relatively little attention, and are clearly in need of more detailed study. Only those which have a bearing on the present interpretation of the area's geological history are discussed below.

Since Langebaanweg is located close to the coast, the local succession has been considerably influenced by past changes in sea-level. Although this succession itself provides evidence of the nature and timing of such changes, these can best be interpreted on the basis of regional and global evidence. Consequently, before proceeding to a more detailed account of deposits in the Langebaanweg area, the record of relevant sea-level movements is examined.

TERTIARY SEA-LEVEL MOVEMENTS ON THE WEST COAST OF SOUTH AFRICA

The nature of the Langebaanweg succession is such that it provides some unique data relevant to the interpretation of southern African sea-level movements. However, since the local record is both complemented and supplemented by evidence from further afield, account will be taken here of such evidence from the approximately 600 km west coast of South Africa. This stretch of coast can conveniently be divided into two regions. They are the south-western Cape coast between False Bay and the Olifants River, and the Namaqualand coast between the Olifants and Orange Rivers (Fig. 1). A coastal plain of varying width fronts on a more or less continuous series of mountains, which separates this plain from an inland plateau.

Shorelines of Cenozoic age are preserved along most of this coast, and much attention has been focused on them, mainly because of associated occurrences of phosphate and diamonds. Although particular reference is made to the shoreline successions in the Langebaanweg area of the south-western Cape and the Hondeklip Bay–Kleinsee section of the Namaqualand coast, successions in other areas may be as well known and as relevant.

There are altimetric similarities between the recorded shorelines of the two regions, and correlations between them, and shorelines elsewhere, have been suggested (e.g. Hendey 1969; Carrington & Kensley 1969). The inter-regional correlations have been modified (Tankard 1975*b*, 1976), while the broader correlations have generally been discounted (e.g. Wolff *et al.* 1973). While the criticism of the latter correlations was justified, more recent studies have indicated that there is a sound basis for correlating the west coast shoreline succession with global phenomena of the Cenozoic. Consequently, broader correlations are feasible. For example, Tankard (1975*b*, 1976) has correlated the lower and more recent of the west coast shorelines with high sea-levels of the last interglacial, and it follows that they are the local equivalents of last interglacial shorelines recorded elsewhere in the world.

This aspect of Tankard's studies is irrelevant here, since it is only the older and higher of the late Cenozoic shorelines which are represented in the immediate vicinity of Langebaanweg. According to Tankard (1975*b*, 1976) the older late Cenozoic shorelines in the south-western Cape are at lower elevations than their counterparts in Namaqualand, this difference being ascribed to differential epeirogenesis along the west coast. However, the difference is here regarded as more apparent than real, and there is, in fact, a remarkable altimetric similarity between all the late Cenozoic shorelines of the two regions.

The Namaqualand succession is both well developed and well documented over a distance of about 400 km, and there has been little disagreement about the elevations of the shorelines constituting this succession. The difference of opinion over the inter-regional correlation centres on the elevation of the higher shorelines in the south-western Cape, and it stems from the nature of the record of these shorelines. The record in the two regions differs simply because of distinctive characteristics in their physical geography.

The Namaqualand coast has a more or less regular north-north-west to south-south-east trend, and, in those areas where ancient shorelines are best developed, it has a bedrock profile which rises at a generally moderate angle from the present shoreline to beyond the limit of the highest late Cenozoic shoreline (c. 100 m). The situation is more complex at the mouths of rivers, where marine and river terraces merge, and where fluvial and estuarine deposits are represented. In general though, the ancient shorelines have a fairly regular development, with associated deposits forming a readily identifiable sequence between 0 and 100 m elevation. The shorelines themselves are generally incised on bedrock. This situation can be largely ascribed to the configuration of the bedrock, and the fact that it is uniformly comprised of 'Namaqualand gneiss' (see Haughton 1968).

By contrast, the coastal area of the south-western Cape is much less regular due to the more complex solid geology (i.e. Basement Complex granites, Malmesbury System metamorphics and intrusives, and Cape Supergroup sedimentary rocks). The more resistant rocks, and those of the relatively young and uplifted Cape Supergroup, form areas of high relief. The bedrock may thus rise steeply from present sea-level to the hills and mountains of the region, although there are also wide areas where bedrock is below present sea-level and where it is overlain by largely unconsolidated late Cenozoic sediments.

The areas of high relief are particularly significant since at times of the higher late Cenozoic sea-levels (c. 50 m and above) those in the east would have formed an irregular and often steep-sided coast, whereas those in the west would have formed two island complexes off the southern and central parts of the region. The islands would also have had irregular and steep-sided coasts, and would have provided some shelter to the adjacent mainland coast from the open ocean. Mechanical erosion by wave action on this coast might, therefore, have been reduced.

Shoreline environments in the south-western Cape, both now and at times of past high sea-levels, thus differ appreciably from those of the Namaqualand coast. Consequently, their features and associated deposits are likely to differ in some respects.

In Namaqualand wave-cut platforms on bedrock, on which gravels and other sediments accumulate, often had their onshore limits marked by notches and low cliffs. In other words, they exhibit many of the classic manifestations of 'raised beaches', and are usually easily identified and differentiated.

The situation in the south-western Cape is by no means as simple. In those areas where bedrock is below present sea-level, wave-cut platforms were developed on unconsolidated deposits. They were, therefore, insubstantial and very susceptible to subsequent erosion. In addition, deposits on the platforms were later to intermingle with essentially similar unconsolidated deposits accumulated under very different circumstances (e.g. subaerially, by aeolian action). Furthermore, gravels would not normally have been deposited on these platforms because of the absence of a source-rock, while notches and cliffs

would also have been absent, with impermanent coastal dunes having been present instead. As a result, evidence of past high sea-levels over wide areas in the south-western Cape may be difficult to detect.

In those areas where bedrock rose steeply into hills and mountains, both on the mainland and on the islands, older and higher notches, wave-cut platforms and superimposed deposits would tend to be undercut and eroded away during subsequent periods when sea-level was at lower elevations. In addition, shoreline features developed on the mainland coast in the lee of the two island complexes might have been relatively insubstantial because of lower-energy waves. Consequently, some of the more obvious manifestations of 'raised beaches' may also be obscured in these areas of the south-western Cape.

It is, therefore, not surprising that surveys have found evidence of the older and higher late Cenozoic shorelines in this region either absent or equivocal.

For example, Davies (1973: 722) believed that there was no direct proof of high shorelines in that part of the south-western Cape which includes the Langebaanweg area (Fig. 2), claiming that 'the existence of pleistocene sea-levels at 90 m and 60 m in [this area seems to be] inferred from these levels in Namaqualand'. The existence of a c. 90 m marine platform in the vicinity of Elandsfontein south-east of Langebaanweg was suggested by Mabbutt (1956), a view subsequently substantiated by Rogers (1980), although he records marine deposits up to an elevation of only about 80 m. This platform is on unconsolidated sediments and is an example of one which lacks some of the classic features of such platforms. The existence of a 50–55 m high sea-level in the vicinity of Langebaanweg has been demonstrated by Tankard (1974a—see p. 40), while Mabbutt (1956: 50) recorded a marine terrace at '45–60 m' 'inland from Saldanha Bay'. This one also lacks the features of the kind that Davies and others have sought.

Davies (1972: 270) also found 'few indications of quaternary shorelines above 30 m' in the southern part of the south-western Cape (i.e. around False Bay and along the southern coast to Gansbaai). However, he does record some evidence of high sea-levels in this area at 45–60 m and 75–94 m. The fact that these records are insubstantial is probably due to the generally precipitous nature of the coast in this area and the destruction of higher shoreline features by subsequent erosion. In addition, the eastern shore of False Bay was sheltered by islands that now constitute the Cape Peninsula.

The fact that there is *some* evidence of these higher shorelines in the south-western Cape is a certain indication that they exist. The evidence for their presence cannot be dismissed because the shorelines are not obvious over wide areas, or because they lack some of the characteristics of shorelines elsewhere. Uncertainty about the actual elevation of the higher shorelines, or discrepancies between recorded elevations in the south-western Cape and Namaqualand do not nullify the correlation between the two regions. They are simply explained by the fact that the south-western Cape record is poorer than that in Namaqualand. In the latter region the stillstands in marine transgres-

sions and regressions are usually determinable, whereas over wide areas of the south-western Cape this is not necessarily the case. In spite of the difference in the nature of the records, elevations for the higher shorelines in the two regions are in remarkably close agreement.

Other Namaqualand shorelines which are supposedly absent or poorly developed in the south-western Cape are those which Carrington & Kensley (1969) recorded at '29–34 m' and '17–21 m'. There is, in fact, unequivocal evidence for a shoreline at *c.* 30 m in 'E' Quarry at Langebaanweg, while there is an indication of a much later high sea-level at about 20 m in the Langebaanweg area (see below), which was probably the one responsible for the 15 m marine terrace recorded in the same area by Mabbutt (1956).

It is worth noting in this connection that Tankard (1975*b*, 1976) has suggested that shorelines recorded at 10 m and 13 m in the south-western Cape may be the equivalent of the 17–21 m shoreline in Namaqualand. He ascribed the lower elevation of the south-western Cape beaches to differential epeirogenesis on the west coast. Since this factor is dismissed here, the discrepancy must have another explanation. It is possible that the 10 and 13 m records in the south-western Cape represent vestiges of a shoreline at a higher elevation (? *c.* 20 m), since features associated with shorelines may extend over appreciable vertical and horizontal distances. Ideally only the maximum elevation of a high sea-level should be recorded (*i.e.* the shoreline itself), but this is not always possible.

It may be significant that, whereas the 17–21 m shoreline is present and well developed at Hondeklip Bay, it is apparently either not represented at Kleinsee, 80 km further north (Hallam 1964), or its deposits are mixed with, and not distinguishable from, those of the older 30 m shoreline. This may be an indication that the stillstand during which the 17–21 m shoreline was developed was not prolonged, and that, consequently, it was only because of some exceptional circumstance of local geography that sporadic records of it have survived. This would be consistent with the nature of the record of the *c.* 20 m shoreline in the Langebaanweg area (see below).

The situation on the west coast of South Africa may be summed up by the statement that there is evidence for four relatively high late Cenozoic shorelines, which are for the sake of convenience referred to by their approximate elevations of 90 m, 50 m, 30 m and 20 m. All represent 'transgressive' or 'regressive complexes' and deposits associated with them may therefore be encountered at elevations above or below those given above.

It has generally been assumed that there is a direct correlation between the age and the elevation of these shorelines, the oldest being the highest, and with elevations decreasing with age. It is evident from the Langebaanweg record that this is not the case. In this area the 30 m shoreline is the oldest, followed in descending order of age by the 90 m, 50 m and 20 m shorelines. The Langebaanweg succession is also important in providing evidence of the actual, or likely, age of these shorelines.

Up until a decade ago it was common practice to suggest correlations between South African shoreline sequences with others elsewhere, notably the classic ones of the Mediterranean Basin, which in turn were correlated with the glacial–interglacial chronology of the Quaternary. Since then the nature and timing of sea-level changes during the late Cenozoic have been much more thoroughly documented, while the complexities imposed by tectonic instability have become more widely appreciated, and the earlier correlations are no longer accepted.

A positive advance in long-range correlation of west coast shorelines came with the studies of Tankard (1975*b*, 1976), who suggested that most, if not all, of the lower shorelines in the south-western Cape date back to the last interglacial. The validity of this conclusion will not be examined here as none of the shorelines is represented in the immediate vicinity of Langebaanweg. At issue though is the age of the older and higher beaches, which have for the most part continued to be regarded as being of Pleistocene age as well. Vertebrate fossils associated with the higher shorelines in the Langebaanweg area indicate beyond all doubt that this succession is largely, or entirely, late Tertiary in age. In addition, the nature of the Langebaanweg fossil assemblages allows for an interpretation of depositional environments which is in good accord with the late Tertiary sea-level movements around southern Africa recorded by Siesser & Dingle (1981). These are in turn in close agreement with the global sea-level changes which were determined by Vail *et al.* (1977). Siesser & Dingle (1981: 83) were concerned only with the ‘gross movements of the seas around southern Africa during the Tertiary’, and details of these movements during the late Tertiary determined on the basis of the Langebaanweg record match those of the global changes (Vail *et al.* 1977; Vail & Hardenbol 1979) remarkably well (Fig. 3).

Siesser & Dingle (1981: 83) summarized the sea-level movements relevant to the Langebaanweg succession as follows: ‘The major Neogene transgression began in the middle Miocene and probably reached its greatest extent in the late Miocene or early Pliocene. The overall middle Miocene to early Pliocene transgression was interrupted by a brief regressive pulse near the Miocene–Pliocene boundary. Seas withdrew again in the late Pliocene.’

The interpretation of global sea-level changes of Vail & Hardenbol (1979) differs slightly in that they have the major Neogene transgression commencing during the early Miocene, reaching a climax early in the middle Miocene, and followed by a middle to late Miocene regression, which took the form of three major drops in sea-level, separated by periods when sea-level was more or less static. The last of these major drops evidently coincides with the ‘brief regressive pulse near the Miocene–Pliocene boundary’ recorded by Siesser & Dingle (1981: 83).

The sea-level movements which affected the Langebaanweg area are referred to in the discussions which follow as:

1. ‘the early to middle Miocene transgression’,
2. ‘the middle to late Miocene regression’, with ‘the terminal Miocene regression’ climaxing this event,

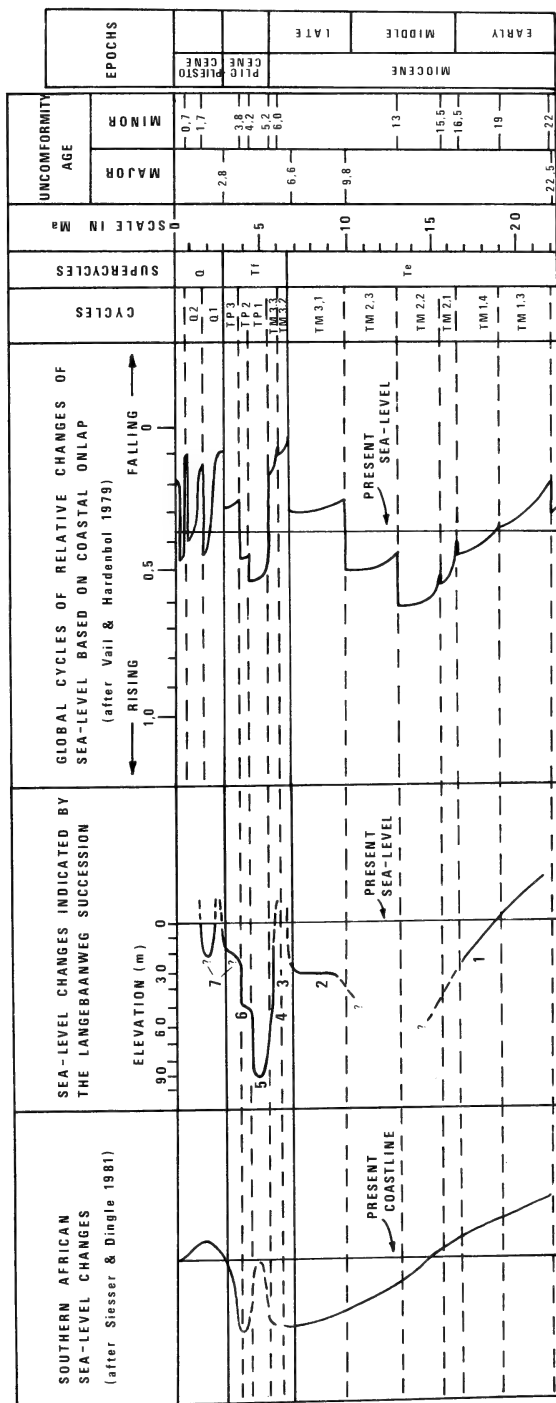


Fig. 3. Records of global and southern African sea-level changes, and those indicated by the Langebaanweg succession. 1. Pre-GM deposits. 2. GM. 3. QSM, PPM. 4. Anyoskop marine deposits. 5. Marine platform south-east of Langebaanweg. 6. Anyoskop terrestrial deposits. 7. Baard's Quarry fluvial deposits.

3. 'the early Pliocene transgression',
4. 'the late Pliocene regression' and 'the early Pleistocene transgression'.

According to the present interpretation of the Langebaanweg succession, deposits beneath the floor of 'E' Quarry ('pre-GM') are associated with the early to middle Miocene transgression; the 30 m shoreline (GM) in 'E' Quarry dates from the middle to late Miocene regression; the 90 m shoreline represents the climax of the early Pliocene transgression, with a large proportion of the deposits in the immediate vicinity of 'E' Quarry having been laid down during this transgression; while the 50 m shoreline represents a stillstand in the late Pliocene regression. The 20 m shoreline is problematical, having been developed either during a second stillstand in the late Pliocene regression, or at the climax of the subsequent early Pleistocene transgression. The reasons for this interpretation will become evident from the discussions which follow in this, and later, sections of this report.

On the basis of the altimetric correlation of south-western Cape and Namaqualand shorelines, it follows that the 29–34 m shoreline in Namaqualand must be of late Miocene age. Carrington & Kensley (1969) believed this shoreline dated from the middle Pleistocene, but there is no firm foundation for this suggestion. The 29–34 m shoreline is represented at Hondeklip Bay, where it is 'thin' and 'discontinuous' (Carrington & Kensley 1969: 190), and at Kleinsee (Hallam 1964), where it is also poorly developed (personal observation). This poor development sets it apart from other elements in the Namaqualand, succession, which suggests that it might have been subjected to erosion during a *subsequent* period when sea-level was at a higher elevation. In other words, it is likely to pre-date the 90 m and 50 m high sea-levels, rather than post-date them as suggested by Carrington & Kensley (1969).

Again on altimetric evidence, the early Pliocene 90 m, late Pliocene 50 m, and the late Pliocene/early Pleistocene 20 m shorelines in the south-western Cape are correlated with the '75–90 m', '45–50 m' and '17–21 m' 'transgressive complexes' in Namaqualand, which Carrington & Kensley (1969: 190–191) dated as 'Basal', 'Lower' and 'Middle Pleistocene' respectively.

According to the above interpretation of west coast shorelines, there are none of middle Pleistocene age. There undoubtedly were glacio-eustatic sea-level fluctuations during this period, and it is likely that during the interglacial phases sea-level was higher than at present, just as it was during the last interglacial, and apparently also during the mid-Holocene. However, Shackleton & Opdyke (1973) have suggested that middle Pleistocene interglacial sea-levels would have been no higher than the highest of the last interglacial levels. Consequently, in tectonically stable area all traces of their presence might have been obscured or destroyed during the last interglacial.

Coastal deposits about which there is some uncertainty are those in the Hondeklip Bay area which in mining terminology are referred to as 'E stage' (Tankard 1975*b*). Although they, too, relate to periods of higher sea-level, they have been regarded as distinct from the deposits of the 'transgressive com-

plexes', and both Carrington & Kensley (1969) and Tankard (1975b) dated them as late Tertiary. Since the higher of the 'transgressive complexes' are here also regarded as late Tertiary, it is necessary to reconsider the age and relationships of the 'E stage' deposits.

The 'lower E stage' deposits were correlated by Tankard (1975b) with the middle Miocene phosphatic rock horizon in 'E' Quarry at Langebaanweg. This correlation is accepted here and the 'lower E stage' is regarded as remnant evidence for the early to middle Miocene transgression on the Namaqualand coast.

The 'middle E stage' deposits were correlated by Tankard (1975b) with the QSM of the Varswater Formation, and this is also accepted here, although the correlation is extended to include the PPM of the Varswater Formation. The QSM and PPM date from the same episode (i.e. the early Pliocene transgression), and there are no grounds for believing that the 'middle E stage' is contemporary with the QSM rather than the PPM.

The age of the 'middle E stage' was partly inferred from remains of two vertebrate taxa which were believed to be derived from this 'stage' and redeposited in younger sediments. One of these taxa, *Ceratotherium praecox*, is represented by a single rolled tooth (Hooijer 1972), which almost certainly is a derived specimen (A. J. Carrington, pers. comm.). The second, '*Prionodelphis*' (= *Homiphoca*) *capensis*, is represented by an isolated canine and a metatarsal. They are unrolled, but Carrington believed them to be derived since they are phosphatized specimens from non-phosphatic deposits. This is not a convincing point of view since phosphatized fossils *in situ* in non-phosphatic deposits have been recorded from 'E' Quarry. A new development concerning the Namaqualand '*Homiphoca capensis*' is that the metatarsal has been found to be appreciably longer than any of the now numerous specimens known from 'E' Quarry. This suggests that the Namaqualand specimen represents a species which was more advanced than the 'E' Quarry *H. capensis*. Consequently, it may well be contemporaneous with the post-'middle E stage' deposits from which it and the isolated canine were recovered.

Other deposits on the Namaqualand coast which were a likely equivalent of the 'middle E stage' were those at Kleinzee from which was recovered the small vertebrate fauna described by Stromer (1931a, 1931b). This fauna is evidently broadly contemporaneous with those from the QSM and PPM at Langebaanweg (Hendey 1974a, 1978c, 1978d).

The 'upper E stage' deposits in the Hondeklip Bay area contain pelletal phosphorite, which led Tankard (1975b) to correlate it with the PPM of the Varswater Formation. While this interpretation cannot be discounted, it is not favoured here. According to one interpretation, the 'E' Quarry pelletal phosphorite is largely derived from a 'mechanical erosion' of the 'Miocene bedded authigenic phosphorite' (Tankard 1975c: 375), and there is no reason to believe that a similar deposit on the Namaqualand coast is necessarily contemporaneous. While it, too, might have been derived from a Miocene phosphorite, the

erosion process in Namaqualand could well have pre- or post-dated deposition of the Varswater Formation PPM. The same applies if the 'upper E stage' and 'E' Quarry pelletal phosphorites are authigenic.

Tankard (1975*b*) records that the 'upper E stage' sediments contain a rich fossil fauna, the molluscs of which indicate warm-water conditions, and that the sediments are recorded only up to an elevation of 30 m. Perhaps significantly, the GM of the Varswater Formation is also comprised of a mechanically eroded Miocene phosphorite, although in the form of a gravel rather than pellet-sized particles, it is also associated with a warm-water mollusc fauna (see p. 68), and it also occurs up to an elevation of 30 m. By contrast, the PPM contains an element which suggests cold-water conditions, and is recorded at elevations well above 30 m.

The 'essentially bedrock-depression infilling' 'upper E stage' (Tankard 1975*b*: 277) may, in fact, represent a part of the 'thin, discontinuous' '29–34 m beach' of Carrington & Kensley (1960: 190), and is recorded as such in Table 2.

The temperature of the adjacent ocean at the time that the various elements in the west coast succession were laid down is of interest. The revised interpretation of the Namaqualand succession means that all those deposits from which warm-water mollusc faunas are recorded date back to the late Tertiary, while those with cold-water faunas are Quaternary.

There are, however, apparent exceptions to this general rule. The 75–90 m shoreline deposits in Namaqualand are unfossiliferous (Tankard 1975*b*), and consequently provide no direct evidence of water temperatures prevailing at that time. However, deposits laid down in 'E' Quarry during an early stage in the 90 m transgression (i.e. the QSM and PPM) contain fossils that indicate cold-water conditions (see p. 68). There is thus likely to have been a similar cold-water fauna on the Namaqualand coast at that time. This period of cold is correlated with the aftermath of the Antarctic glacial maximum during the terminal Miocene (see p. 70). Since the 90 m early Pliocene transgression post-dates this glacial maximum, it is possible that cold conditions prevailed only during the early stages of the transgression, and that by the time it reached its peak sea temperatures were higher.

Tankard (1975*b*) recorded that the 17–21 m shoreline in Namaqualand is associated with a cold-water fauna. If this shoreline is late Pliocene in age, then it would be an exception to the 'late Tertiary/warm water' rule. On the other hand, this may be interpreted as evidence that the 17–21 m shoreline dates from the early Pleistocene, which would be in keeping with evidence from the Langebaanweg area (see p. 41).

Although the present study was confined to the shorelines on the west coast of South Africa, it is obvious that a similar reinterpretation of coastal successions elsewhere in southern Africa is possible. For example, according to the present interpretation and contrary to earlier opinion, the 'Upper Terraces Group' on the southern coast of the Namib Desert, with their warm-water faunas (Hallam 1964), are likely to be late Tertiary in age.

TABLE 2

Records of late Tertiary and early Pleistocene sea-level changes on the west coast of southern Africa.

AGE	TRANSRESSION OF REGRESSION	SEA-LEVEL CYCLES (1)	SOUTH-WESTERN CAPE (2)	HONDEKLIP BAY (3)	KLEINZEE (4)	SOUTHERN NAMIB DESERT (4), (5)
Early Pleistocene	T	Q1	20 m (Baard's Quarry fluvatile) ↓	17-21 m ↓	? in part ← ↓	? ← ↓
Late Pliocene	R	TP3	? ↓	? ↓	? ↓	? ↓
		TP2	50 m (Anyskop terrestrial)	45-50 m	40-64 m	15 m (E Beach)
Early Pliocene	T	TP1	90 m (‘E’ QSM, PPM; Anyskop marine)	75-90 m (? including ‘middle E stage’)	82-88 m	20-25 m (F Beach)
Terminal Miocene	R	TM3.2, TM3.3	No deposits	No deposits	No deposits	No deposits
Late Miocene	R	TM3.1	30 m (‘E’ GM)	29-34 m (? including ‘upper E stage’)	21-40 m —	12 m — (D Beach)
Middle Miocene	T	TM1.3-TM2.2	Pre-GM	‘lower E stage’		33 m (‘false bed- rock gravels’ and Arrisdrift fossil site)

(1) Vail & Hardenbol (1979). (2) Langebaanweg area (this report); complementary data from Davies (1972, 1973), Tankard (1974a) and Rogers (1980). (3) Carrington & Kensley (1969) and Tankard (1975b). (4) Hallam (1964) and Corvinus & Hendey (1978). (5) Downwarped coast—terraces at lower elevations than those on South African coast.

The poorly developed 'D Beach' (12 m) of the 'Upper Terraces Group' is here tentatively correlated with the late Miocene 30 m shoreline on the South African west coast, although it could instead be the equivalent of the late Pliocene 20 m shoreline. The latter alternative is less likely because the 20 m shoreline is apparently associated with a cold-water fauna (see above). In addition, the poor development of the 'D Beach' may be an indication of erosion during a subsequent high sea-level, which was suggested in the case of the 30 m shoreline on the South African west coast.

The 'F Beach' (25 m) and 'E Beach' (15 m) are here correlated with the South African west coast 90 m and 50 m shorelines.

The 'false bedrock gravels', which extend northwards from the mouth of the Orange River, evidently pre-date the 'Upper Terraces' (Hallam 1964), and could therefore date back to the middle Miocene. They are the likely equivalent of the pre-GM deposits at Langebaanweg and the 'lower E stage' of the Namaqualand coast. In addition, they are probably the coastal equivalent of the middle Miocene river terrace(s) at Arrisdrift, 30 km inland from the mouth of the Orange River (Corvinus & Hendey 1978; Hendey 1978*b*). It is worth noting in this connection that the bedrock elevation of the channel which contains the middle Miocene fossils at Arrisdrift is 40 m, while the river level is 7 m above sea-level. It follows that their coastal equivalent should be at 33 m, which is, in fact, the elevation of the base of the cliff against which the 'false bedrock gravels' are banked (Hallam 1964). It may also be significant that while there are four river terraces recognized at Arrisdrift (Corvinus & Hendey 1978), there are also four marine terraces of late Tertiary age on the coast (i.e. the 'D', 'E' and 'F' Beaches and the 'false bedrock gravels').

The Arrisdrift fossil occurrence is of particular significance in the interpretation of the southern African west coast succession, since it provides the most reliable evidence of the time at which the early to middle Miocene transgression began to result in deposition on the present coast. The Arrisdrift fossils date back about 16 Ma (Hendey 1978*b*), that is, to the early part of the middle Miocene.

The correlation of the west coast shorelines suggested here is summarized in Table 2.

GEOLOGICAL HISTORY AND DEPOSITIONAL ENVIRONMENTS OF THE LANGEBAANWEG SUCCESSION.

As indicated earlier, the Langebaanweg succession is most conveniently interpreted in relation to the southern African sea-level changes recorded by Siesser & Dingle (1981).

The pre-Miocene sea-level changes

There is no evidence in the Langebaanweg area (Figs 2,4) for any deposits dating back to the early Tertiary. Two marine transgressions are recorded

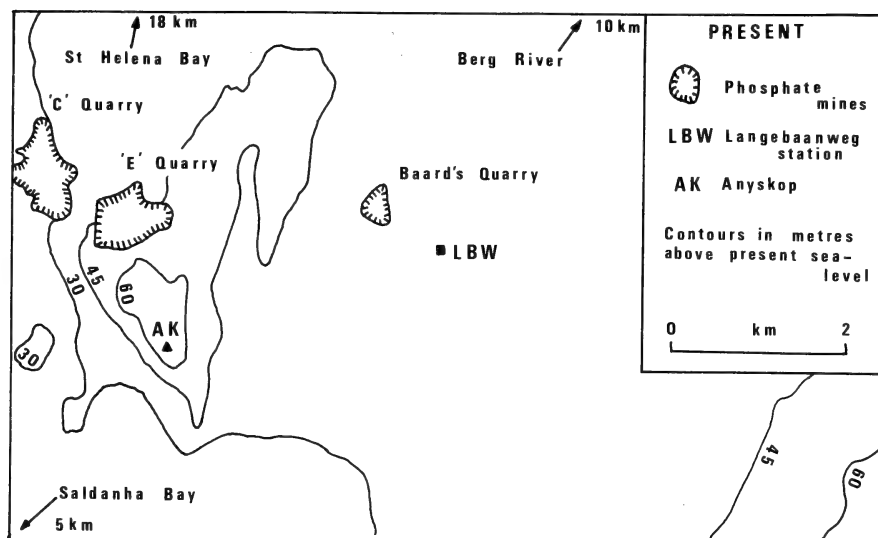


Fig. 4. The Langebaanweg area today.

during this period, one in the late Paleocene/early Eocene and the other in the late Eocene (Siesser & Dingle 1981).

There are records of Eocene marine deposits at 70 and 163 m on the west coast in the southern Namib Desert (Bogenfels and Buntfeldschuh—Siesser & Dingle 1981), as well as possible Eocene deposits at about 140 m at Buffels Bank (Kamaggas) west of Springbok (South African Museum records), and of uncertain elevation at Quaggaskop near Vanrhynsdorp (Lamont 1947). If the latter records are indeed Eocene, then the shorelines of this period must have abutted the western escarpment in Namaqualand, whereas in the downwarped southern Namib they approached the present coast near Bogenfels following the east-west trend of the Klinghardt Mountains in this area (Fig. 1). The implication is that during the Eocene transgressions much of the south-western Cape, including the Langebaanweg area, was below sea-level, the coastline being along higher ground many kilometres east of Langebaanweg.

There was then a major regression spanning the entire Oligocene, and much or all of the early Miocene, when sea-level reached several hundred metres below that of the present (Siesser & Dingle 1981). This is likely to have been the period of major continental erosion during which all traces of early Tertiary sediments in the Langebaanweg area, and elsewhere along the west coast, were removed. It might have been during this period that the bedrock in the Langebaanweg area was eroded down to its present elevation of about -40 m.

The early to middle Miocene transgression

The presence of early Miocene vertebrates in fluvial and lacustrine deposits near the coast of South West Africa between Bogenfels and Lüderitz

(Stromer 1926; Hopwood 1928; Hamilton & Van Couvering 1977; Hendey 1978*b*) is a possible indication that at least this section of the west coast was then being influenced by the early to middle Miocene transgression. The southern Namib region was certainly being influenced by this transgression early in the middle Miocene, when the fossil assemblage at Arrisdrift was deposited on a river terrace (Corvinus & Hendey 1978; Hendey 1978*b*). Apparently contemporaneously the 'false bedrock gravels' of the southern Namib coast were being laid down, and these are in turn correlated with the 'lower E stage' and related deposits on the Namaqualand coast, and the pre-GM deposits in the Langebaanweg area.

The pre-GM deposits are known only from boreholes, although small exposures of their uppermost levels formerly existed in 'C' and 'E' Quarries. About 70 m of these deposits are now known, ranging in elevation from about -40 m to +30 m (Rogers 1980), although until recently only the upper 15-20 m had been placed on record (Tankard 1975*b*). The sequence is apparently comprised largely of deposits laid down under terrestrial environments, but at least in the case of the upper levels studied by Tankard (1975*b*: 34), 'it is likely that these deposits formed close to sea level' during 'a slow transgression'. Tankard found evidence in the sequence of a 'marine incursion', which was 'a minor event of very short duration . . . readily explained by breaching of a barrier'. A second marine incursion 'was accompanied by phosphate mineralization to form a phosphatic sandstone' (Tankard 1975*b*: 34).

Peats in the succession have yielded abundant pollens which indicate a forested environment, including subtropical elements such as palms (J. A. Coetzee, pers. comm.), which was very different from the treeless sclerophyll (fynbos) vegetation of the area today. Macroplant remains also include remnants of trees. The plant fossils provide no direct evidence of age, but the vegetation is consistent with a local one of Miocene age (Coetzee 1978).

The phosphatic sandstone mentioned above is recorded up to an elevation of 30 m, and is a significant element in the succession. It contributed to Tankard's (1975*a*: 262) dating of at least this element as 'middle Miocene (Langhian)', and provided some indication of the likely marine environment at the time that it was developed (Tankard 1974*a*; Birch 1977). In addition, its resistant nature served to protect the underlying deposits from erosion during the marine regression that followed during the late Miocene.

The 30 m elevation of the phosphatic sandstone recorded in 'E' Quarry does not necessarily reflect the maximum elevation reached by the early to middle Miocene transgression. If this phosphatic rock formed in an open shelf environment as suggested by Birch (1977, fig. 4), then the 'E' Quarry area might have been as much as 200 m below the sea-level of that time.

Another indication that this transgression reached an elevation substantially higher than 30 m is the presence on the southern Namib Desert coast of apparently contemporaneous deposits at 33 m (Table 2). It is evident from the elevations of the late Tertiary shorelines post-dating the 33 m terrace that there

has been appreciable downwarping of this coast. For example, the suggested equivalent of the 90 m early Pliocene shoreline on the South African west coast is at an elevation of only 20–25 m in the southern Namib Desert, and drops to even lower elevations northwards from the Orange River (Table 2; Hallam 1964). The implication is that the 33 m terrace is now also much lower than its as yet unrecorded counterpart on the South African west coast.

It is, therefore, unlikely that the 30 m record at Langebaanweg and the 33 m record in the southern Namib represent the maximum elevation of the early to middle Miocene transgression. There is apparently no way of determining this elevation on the basis of available evidence, and this is reflected in the Langebaanweg record represented in Figure 3. However, it is possible that the ?Eocene marine deposits at Buffels Bank and Quaggaskop in Namaqualand (see p. 19) are, in fact, of middle Miocene age. The former are at an elevation of about 140 m, and although the elevation of the Quaggaskop deposits is uncertain, it is apparently about 120 m. The middle Miocene transgression might therefore have reached an elevation in the order of 120–140 m.

The middle to late Miocene regression

The middle to late Miocene regression affected the Langebaanweg area by causing erosion of deposits laid down during the preceding transgression. The middle Miocene phosphatic sandstone exposed in 'C' and 'E' Quarries, and encountered in boreholes to the south and south-west of these quarries, was reduced by wave action to a gravel comprising pebble-, cobble- and boulder-sized elements. The north-easterly limit of this gravel, which was briefly exposed in trenches on the floor of 'E' Quarry during 1972, occurs at an elevation of about 30 m. The gravel itself forms the basal unit of the Varswater Formation (i.e. the Gravel Member—GM).

The GM evidently had a complex history. For example, Butzer (1973: 238) recognized five stages in its development, excluding the formation of the original phosphatic sandstone. They are:

1. 'Reworking of [the primary middle Miocene] phosphatic rock.'
2. 'Induration of the previous agglomération with phosphate' to form what is here termed the secondary phosphatic rock of the GM (Fig. 5).
3. 'Reworking of this new generation of [phosphatic rock] into cobbles and blocks.'
4. 'Partial carbonate cementation and iron-enrichment of the previous agglomerate'.
5. 'Reworking of all the previous products of induration into a matrix of unconsolidated, white (10YR) medium-to-coarse-grade sands.'

Assemblages of marine fossils indicative of sandy and rocky beach environments occur in the secondary phosphatic rock (stage 2), and in the unconsolidated sands (stage 5). These were termed 'Marine Faunal Units 1 and 2' respectively by Hendey (1974a), and their invertebrate components were

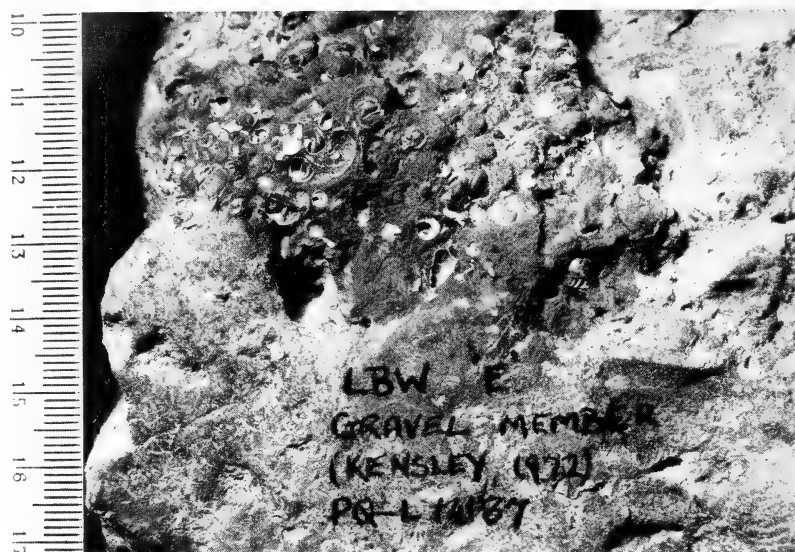


Fig. 5. A Gravel Member (GM) boulder of primary phosphatic rock (labelled section), encrusted with fossiliferous secondary phosphatic rock.

described by Kensley (1972), with some additional taxa having been recorded by Tankard (1974a, 1975b).

Evidently an appreciable period of time elapsed between stages 1 and 5 in the development of the GM, and throughout this period the deposits must have been at, or near, sea-level. Since the primary phosphatic rock might also have been formed in a similar environment, it is possible that sea-level was at an elevation of about 30 m for much of the middle to late Miocene.

However, this interpretation is not favoured and it seems much more likely that the early to middle Miocene transgression, during which the primary phosphatic rock was formed, reached a much higher elevation, as indicated above.

Another possible interpretation of the history of the GM is that it developed during a temporary stillstand in the middle to late Miocene regression. According to Vail & Hardenbol (1979) this regression was interrupted by two periods when sea-level was nearly static, one between 13 and 10 Ma (cycle TM2.3 of supercycle Te), and the other between 10 and 6,6 Ma (cycle TM3.1 of supercycle Te). Sea-level during the former period was comparable to that during the Langhian (Vail & Hardenbol 1979: fig. 8), the age when the primary phosphatic rock was formed (Tankard 1975a), and this coincidence, coupled with the coincident occurrence of the primary and secondary phosphatic rocks in 'E' Quarry, may indicate that the GM dates from cycle TM2.3. On the other hand, the elevation of the GM relative to that of subsequent high sea-levels recorded in the Langebaanweg area suggests that the GM was developed during the cycle TM3.1, that is, immediately prior to the terminal Miocene regression.

It is also possible that one or more of the later stages in the development of the GM took place during the subsequent early Pliocene transgression. While this possibility cannot be dismissed, it is not favoured here, because both invertebrate assemblages of the GM include warm-water taxa, suggesting sea temperatures consistent with the late Miocene, whereas at least during the early stages of the early Pliocene transgression sea temperatures were lower (see p. 16). In addition, the repeated reworking of previous products of deposition observed by Butzer (1973) is more consistent with a regression than a transgression.

A considerable amount of attention has been focused on the origin and age of phosphatic deposits, including those in South Africa (e.g. Tankard 1974b; Birch 1977; Siesser 1978) and further investigation of the primary and secondary phosphatic rocks of the GM may provide additional evidence relevant to the history of this horizon. Tankard's (1975a) belief that the phosphatic rock horizons on the west coast are all of middle Miocene age is now discounted (Siesser 1978; Dingle *et al.* 1979). This probably is indeed the age of the primary phosphatic rock represented in the GM, but the secondary phosphatic rock may be appreciably younger. Siesser (1978) has concluded from evidence on the South African continental shelf that phosphate deposition also occurred during the late Miocene and into the Pliocene. Although there is at present no direct evidence linking this period of phosphate deposition with the secondary phosphatic rock, such a link would be consistent with the inferred late Miocene age of the GM.

It was suggested elsewhere (Hendey 1976a) that the GM includes some fossils derived from pre-existing deposits. This suggestion was based on the belief that the GM was broadly contemporaneous with the overlying QSM and PPM, and the presence in the GM of some teeth tentatively identified as belonging to the late Miocene horse, *Hipparion primigenium* (Hendey 1976a), which is distinct from the *H. cf. baardi* and *H. cf. namaquense* found in overlying deposits (Hooijer 1976). However, now that the GM is interpreted as a late Miocene deposit, the *H. cf. primigenium* teeth may well be contemporaneous with its deposition. If so, then the GM can be no older than 12.5 Ma, the earliest date at which *Hipparion* could have entered Africa (Churcher & Richardson 1978).

The reworking and accumulation of deposits constituting the GM ceased with the retreat of the sea from the Langebaanweg area, probably at the time of the terminal Miocene regression. Tankard (1974a) suggested that this retreat was caused by the development of a sandbar to the south of 'E' Quarry during a temporary stillstand in the transgression which led to the deposition of the Varswater Formation. Tankard has demonstrated that such a bar did, indeed, exist during the period of deposition of the QSM and PPM, while it is certain that these elements in the succession were deposited during a transgression. However, the stillstand postulated by Tankard is here interpreted as a regression (i.e. the terminal Miocene one), and it is believed that the bar was built up

only during the subsequent transgression (i.e. the early Pliocene one), when a river began feeding sediment into the area.

The interpretation of the sea-level history at that time as 'transgression-regression-transgression' over a prolonged period, rather than a shorter period of 'transgression-stillstand-renewed transgression', was the key to the correlation of the 'E' Quarry succession with certain global events of the late Miocene and early Pliocene (see p. 70). This, in turn, suggested a correlation with the record of sea-level movements around southern Africa as interpreted by Siesser & Dingle (1981), and to the global sea-level changes recorded by Vail *et al.* (1977) and Vail & Hardenbol (1979).

Hitherto the deposits of 'E' Quarry have been interpreted as having been laid down during a single transgression, probably that which resulted in deposition of Dingle's (1971, 1973) unit T₄ (e.g. Bishop 1980). The revised interpretation of events indicates that while the QSM and PPM are referable to T₄, the underlying deposits correlate with unit T₃. These units are respectively correlated with sea-level supercycles Tf and Te of Vail & Hardenbol (1979).

The early Pliocene transgression

Introduction

Whatever the history of the GM and the period immediately following its deposition, it is clear that thereafter there was a major change in the local environment. This was brought about by another marine transgression, during the early stages of which a river met the sea in the immediate vicinity of 'E' Quarry and was responsible for discharging most of the sediment making up the QSM and PPM of the Varswater Formation. The nature of these sediments was dependent on the position of the river channel, which moved northwards as the transgression progressed.

The QSM and PPM are by far the best documented deposits in the Langebaanweg area (Table 3). The largest assemblages of fossils from this area are from these deposits and they provide the evidence of age (*c.* 5.0 Ma) which indicates their association with the early Pliocene transgression (see p. 94). Judging from fossil evidence and the likely relationship of these deposits to others in the vicinity, the QSM and PPM date from the earlier part of this transgression. The earliest phase in this transgression is not represented by deposits in the area, while towards its climax the area was largely, or entirely, inundated by the sea. The only surviving record of local deposition during the latter period are some of the deposits making up Anyskop, which overly the PPM south of 'E' Quarry.

Three distinct positions have been recognized for the lower course of the river during the period of deposition of the QSM and PPM. There were intervals of undetermined duration between the successive positions of the river channel. These intervals are reflected by evolutionary changes in taxa common to more than one set of deposits associated with the channel positions (Hendey 1978*d*, 1980; Gentry 1980; De Muizon & Hendey 1980).

When the QSM was laid down, the river channel was to the south-east and south of 'E' Quarry, its estuary being immediately north of the sand-bar recorded by Tankard (1974a) (Figs 6–7). The configuration of the estuary and the bar separating it from the sea was then probably similar to the analogous area of the Berg River today, the principal difference being in the position of the sea relative to the estuary. The sea is to the north of the present estuary, which has a north-east to south-west trend, but in QSM times the bar had a more or less east to west trend, with the sea to the south.

The second position of the channel was about 500 m further north, and it cut diagonally across 'E' Quarry from north-east to south-west. The northward movement of the channel was probably caused by the transgressing sea breaching the sand-bar. The fossiliferous deposits of the second channel constitute bed 3aS of the PPM, while other largely unfossiliferous deposits make up part of the undifferentiated element of the PPM. These deposits were laid down over the QSM, filling the area north of the original bar. The extent of the bar was thus considerably increased, both vertically and horizontally (Fig. 7). The sea-floor beyond the river mouth was marked by a submarine channel (Fig. 6).

Later still the channel shifted northwards again, but this time the change was slight. It might have affected only a relatively short section of the river, perhaps as little as the last kilometre from its mouth, with the mouth itself probably remaining in essentially the same position as in bed 3aS times. The new channel still had a north-east to south-west trend, although once beyond the northern perimeter of the quarry it swung southwards and truncated the south-westerly parts of bed 3aS (Fig. 6). The deposits of the third channel, and associated fossiliferous ones, constitute bed 3aN of the PPM, and once again contemporary unfossiliferous deposits are included in the undifferentiated element of the PPM.

Thereafter, the river must have continued to discharge sediment (PPM undifferentiated) into the area for a while, but as the transgression progressed, the river mouth must have moved further north or east from the 'E' Quarry area, with a consequent diminution in the influence of the river on local sedimentation. At the time of the climax of the transgression (90 m), the river mouth must have been many kilometres away. The final extent of local deposition at this time cannot be determined since the PPM in 'E' Quarry, and to the north and east, was truncated to a maximum of 50–55 m by erosion during the subsequent late Pliocene regression. The only other recorded local deposits dating from the early Pliocene transgression were some of those comprising Anyskop (see below).

It has previously been assumed that the progressive northward shift in the river channel during QSM and PPM times was caused by the rise in sea-level during the transgression. A second factor involved may have been the build-up in a northerly direction of the sand-bar separating the estuary from the sea. Substantial sedimentation was then taking place, and this, together with the rising sea, might have affected the lower course of the river, especially in the case of the slight change from bed 3aS to bed 3aN.

TABLE 3
Depositional environments, characteristic sediments and fossil occurrences in the QSM and PPM of the Varswater Formation, 'E' Quarry, Langebaanweg.

Dingle <i>et al.</i> 1979	Hendey 1980 and this report	DEPOSITIONAL ENVIRONMENTS	CHARACTERISTIC SEDIMENTS	FOSSIL OCCURRENCES	
A-C D1	PELLETAL PHOSPHORITE MEMBER	PPM, undifferentiated	marine littoral	phosphatic sand	some marine microfossils, vertebrates very rare
		I	river bank	clayey sand on phosphate rock	fossils abundant; seals and terrestrial vertebrates predominant
		II	river channel	quartz sand and fossil lag on, and in lee of phosphate rock	fossils abundant; seals and terrestrial vertebrates predominant
III		intermediate between II and IV	quartz sand and fossil lag grading into carbonaceous sand and clay	fossils common; seals and terrestrial vertebrates predominant	
D2	IV	marsh and pond	carbonaceous sand and clay, sometimes under quartz sand and clay horizons	fossils progressively less common south of III; only vertebrates recorded, but pollens probably present	
	not sub-divided	river channel and river bank	quartz sand and fossil lag grading upwards into phosphatic sand	fossils abundant, but becoming less common in phosphatic sand; terrestrial vertebrates predominant	
D4	PPM, bed 3aS				

E1	QUARTZOSE SAND MEMBER		QSM	I	floodplain, with associated microenvironments (e.g. pond, minor drainage channel)	quartz sand	fossils sometimes abundant; terrestrial vertebrates predominant
				I(A)	possible variation of I, ? floodplain closer to river channel	quartz sand	fossils sometimes common; terrestrial vertebrates predominant
				II	marsh	carbonaceous sand and clay	fossils abundant; pollens predominant, terrestrial vertebrates common
				III	tidal flats	muddy silt	fossils abundant; marine, estuarine and freshwater invertebrates predominant
E4				(IV)	? river channel (not exposed but probably exists south-east and south of quarry)	not known	not known

Note. The subdivisions D2 and D3 and E1 to E4 (and their equivalents, PPM 3aN I to IV and QSM I to IV) are facies of sedimentary units (see Dingle *et al.* 1979, fig. 5).

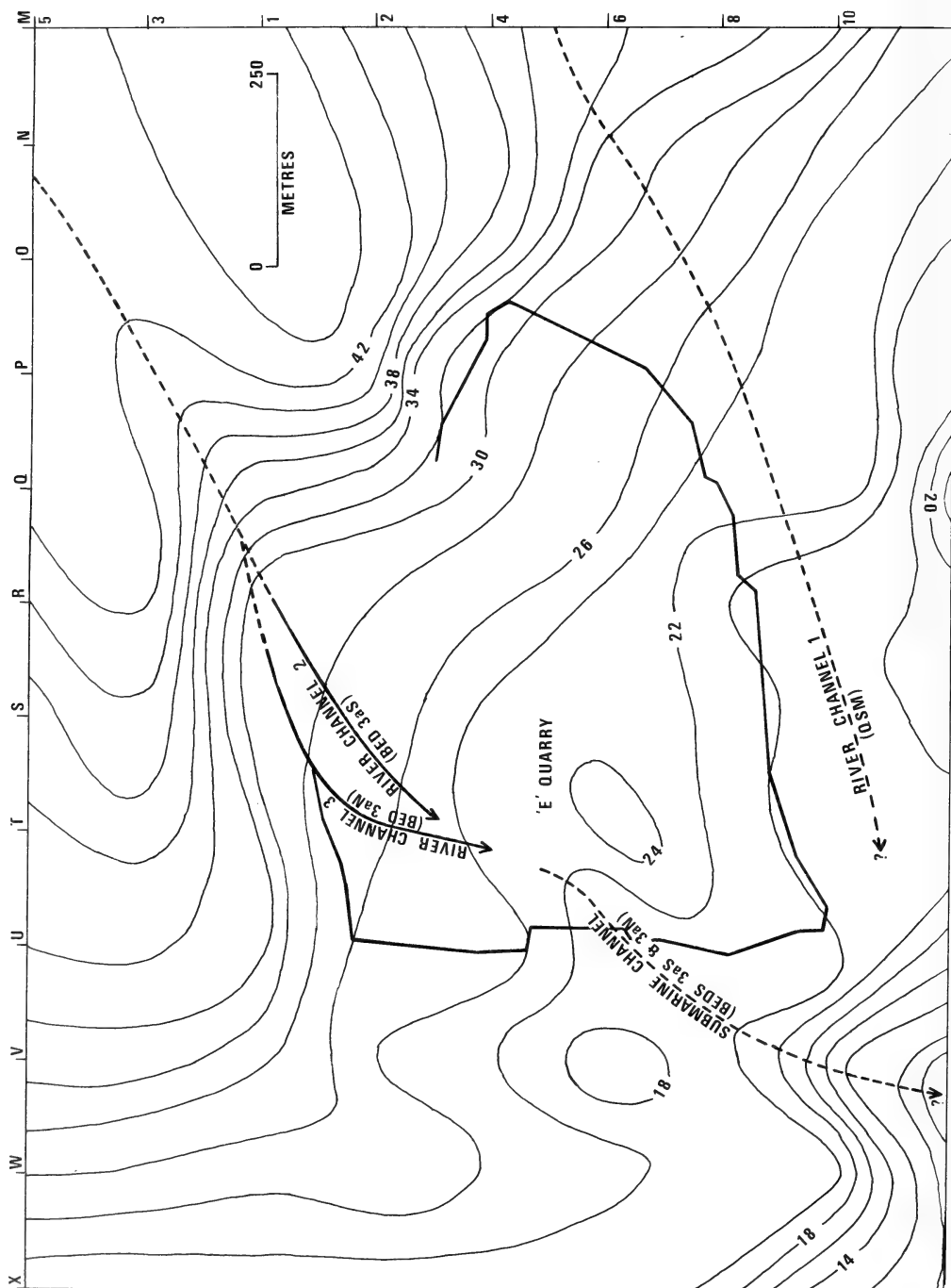


Fig. 6. Structure contour map of the base of the Pelletal Phosphorite Member (PPM). Arrowed lines indicate inferred positions of the river channels and a submarine channel at the times when the Quartzose Sand Member (OSM), PPM 3aS, and PPM 3aN were laid down. (Adapted from Tankard 1974a, Fig. 3.)

While the bed 3aS deposits overlie and are generally at a higher elevation than those of the QSM, the situation in respect of bed 3aN relative to bed 3aS is more equivocal. Some of the bed 3aN deposits are higher than any of bed 3aS, but nowhere was the former clearly superimposed on the latter. In fact, there was a lateral (westerly) truncation of bed 3aS by bed 3aN, and both were superimposed on the QSM (Fig. 6, Table 8).

The actual elevation of sea-level when the river was in its various positions cannot be accurately determined. The fossiliferous deposits of the QSM and PPM range between elevations of 30 m and 40 m, which is a possible indication of the magnitude of the sea-level rise which took place during their deposition. However, the actual rise might have been less, since much of the deposition associated with the 3aS and 3aN channels apparently took place during floods when river levels were high. Not even the elevation of the QSM tidal mudflat bed (QSM I—Table 3) is of assistance in resolving this issue, partly because this bed was truncated by overlying deposits, and partly because nothing is known of the local tidal range at that time. This range may have been large because of the estuarine situation of the mud-flat bed. The complex nature of tides in estuaries is well known, with ranges being markedly affected by the volume and strength of the river flow. In addition, it is possible that at the time that the QSM was laid down, the sea connection between the present Saldanha and St Helena Bays was incomplete, in which case the ancient Berg River, with its seasonal floods, would have discharged into a large bay, a combination of circumstances which can also affect tidal ranges.

The QSM

The first of the three positions of the river channel was not exposed in 'E' Quarry, although it is possible that some of the deposits in the south and south-east of the quarry were laid down in an enlarged flood-season channel. The proximity of the channel to this area is indicated by the nature of the deposits in the south-central part of the quarry, and, to a lesser extent, by other exposures of the QSM on the floor of the quarry. Three main depositional environments (i.e. facies) of the QSM are recognized. All were truncated during the initial stages of the deposition of overlying deposits and their original depth and areal extent can no longer be determined. Each of the facies is characterized by distinctive sediments and fossil assemblages (Table 3).

In the south-central part of 'E' Quarry there survives the vestiges of a tidally inundated mud-flat bed (QSM III of this paper, or Layer E3 of Dingle *et al.* 1979). The fossil assemblage of this muddy silt includes an extensive invertebrate assemblage which was described and discussed by Kensley (1977). Vertebrate remains are rare and are comprised mostly of small bone fragments washed in from elsewhere. The most remarkable of the non-invertebrate fossils are fragments of bird egg-shell, which, like some of the invertebrates, retain traces of their original colour. The invertebrates include terrestrial, freshwater, estuarine and marine species, and comprise an assemblage typical of a mud-flat environment (Kensley 1977).

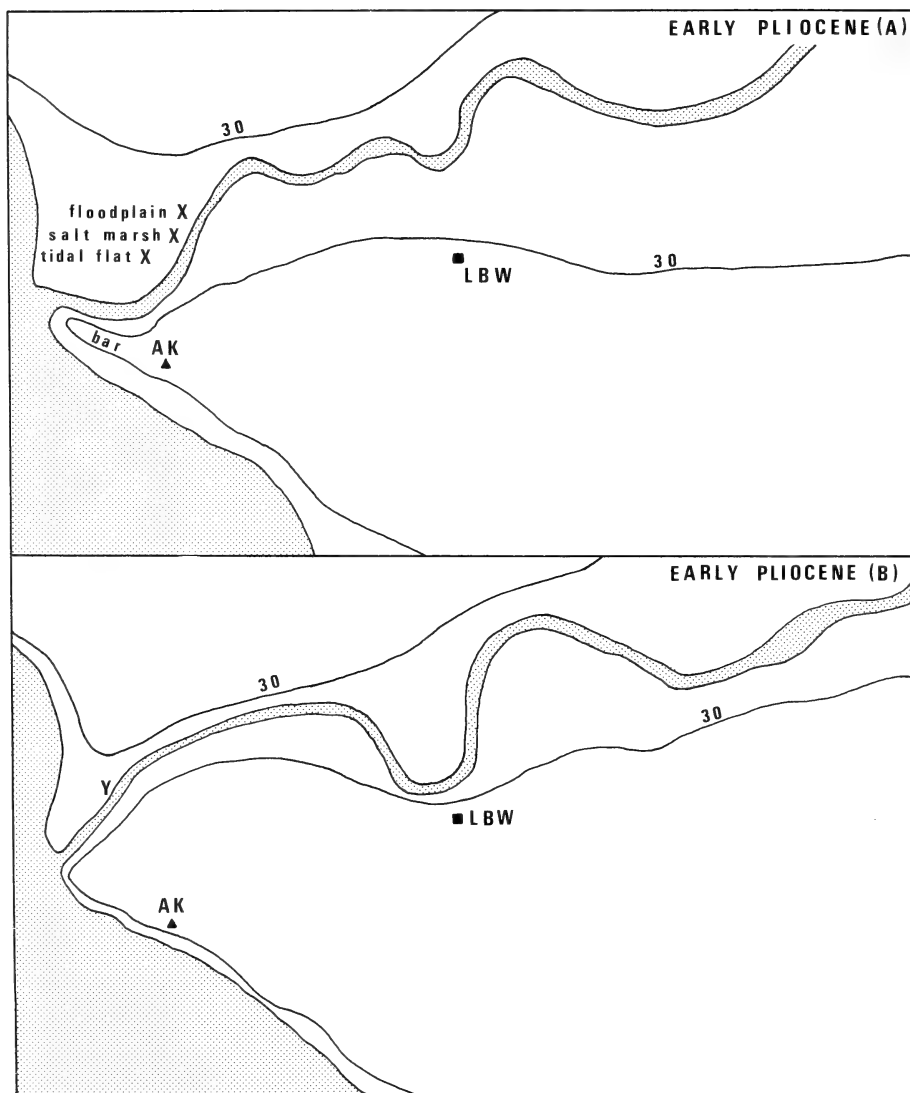


Fig. 7. The Langebaanweg area during the early Pliocene (sea-level cycle TP1). A. Period of deposition of the QSM (X-E Quarry exposures of the QSM). B. Period of deposition of the PPM 3aN (Y-E Quarry exposures of the PPM 3aN). (See Fig. 4 for key.)

Immediately adjacent to the mud-flats bed, largely in a north-easterly direction, is the more extensive 'peat' bed of the QSM (QSM II of this paper, or Layer E2 of Dingle *et al.* 1979). These black, carbonaceous sands and clays represent a marsh deposit. Their fossil content has yet to be analysed in detail, but they are rich in both pollens and vertebrate fossils. They were briefly discussed by Hendey (1976a: 225-226) and Rich (1980).

Elsewhere to the north-west, north, north-east, and east are exposures of the quartzose sands which are the main component of the QSM (QSM I of this paper, or Layer E1 of Dingle *et al.* 1979). These deposits apparently accumulated on the floodplain of the river, and were therefore partly subaerially and partly subaqueously deposited (Hendey 1974a: 32–33, 35–36, 349–353; 1976a: 223–224). It is believed that the inundation of these deposits during flood periods was gentle rather than torrential. In other words, the area was not affected by the strong currents in, and immediately adjacent to, the main river channel, but was inundated by slow-moving backwaters which overflowed from the main channel.

The representation of fossils in QSM I is variable both in terms of condition of specimens and associations of taxa. Apart from indicating the subaerial and subaqueous conditions of dry and wet seasons respectively, they suggest the existence of such microenvironments as ponds and minor drainage channels (Hendey 1976a: 223, 226). Terrestrial vertebrates predominate, and there is good evidence that at least some, and perhaps even most, were subaerially accumulated (Hendey 1974a: 351; 1976a: 224). On the other hand, some subaqueous deposition also took place, together with subaqueous disturbance of previously deposited materials. This would account for the occasional presence of aquatic species in association with terrestrial ones, and the nature of certain of the occurrences.

Although a wide variety of taxa are represented in QSM I, the most characteristic are a tortoise (*Chersina* sp.), a francolin (gen. and sp. not determined), a rhinoceros (*Ceratotherium praecox*), a pig (*Nyanzachoerus* cf. *pattersoni* (or *kanamensis*)), and a boselaphine antelope (*Mesembriportax* (or *Miotragocerus*) *acrae*). The tortoise is the most commonly represented of these taxa. Remains of this animal were sometimes present in astonishing quantity, and they occasionally occurred where no other fossils were obvious (see p. 78).

While much of QSM I was probably deposited some distance from the main channel of the river, this was not the case with the more southerly and south-easterly exposures. Here there are areas of coarser-grained sands, as well as clayey sands, while the associated fossils differ in both condition and species representation. Amongst the species recorded from these deposits are a seal (*Homiphoca capensis*) and giraffids (*Giraffa* sp., *Sivatherium hendeyi**), which are otherwise characteristic of QSM II and the channel deposits of the PPM. The seal is known from elsewhere in QSM I, but there it is represented mainly by the remains of very young individuals, whereas in the other deposits mentioned above, sub-adults and adults predominate. The latter probably died in, or near one of, their natural habitats (i.e. the river channel), whereas the very young ones of QSM I might have been carried away from their nursery by terrestrial carnivores.

To sum up, the QSM was laid down when the river channel was largely to the south and south-east of 'E' Quarry, where it was separated from the sea by a sand-bar (Fig. 7). Remnants of a tidal mud-flat deposit laid down on the

* Churcher (1978) suggested that *S. hendeyi* is conspecific with *S. maurusium*, but it is here regarded as sufficiently distinct to warrant separate specific status.

northern margins of the estuary are preserved, as are remnants of an immediately adjacent salt marsh. Elsewhere there are deposits which were inundated by floods during the wet season. The picture that emerges is the almost classic one of an estuarine environment and its associated sedimentary facies. The present Berg River estuary appropriately provides an ideal modern analogue.

Perhaps the most significant characteristic that distinguishes the QSM from the PPM is that the former are non-phosphatic. This is simply explained by the fact that the development of authigenic phosphate did not occur in those facies of the QSM exposed in 'E' Quarry (i.e. floodplain, salt marsh and tidal flat). However, there evidently was phosphate deposition in other local environments which existed at the time that the 'E' Quarry QSM deposits were laid down. For example, the deposits comprising the sand-bar which separated the estuary from the sea are phosphatic (Tankard 1974a), as are those which accumulated in the marine littoral environment. The latter environment encroached on the 'E' Quarry exposures of the QSM as the transgression progressed, and resulted in the deposition of the PPM in this area. There was a coincident north-easterly migration of the estuarine facies in this depositional system (i.e. the QSM).

The QSM and PPM therefore represent lithostratigraphic units, and not chronostratigraphic units (Fig. 8), and may be termed 'magnafacies', while any chronostratigraphic units which may yet be defined would be termed 'parvafacies' (see Krumbein & Sloss 1963: 320, fig. 9-6). It is fortuitous that none of the PPM deposits laid down contemporaneously with the QSM have yet been exposed in 'E' Quarry, while the QSM counterparts of the 'E' Quarry PPM deposits are also not exposed, and may, in fact, no longer be preserved.

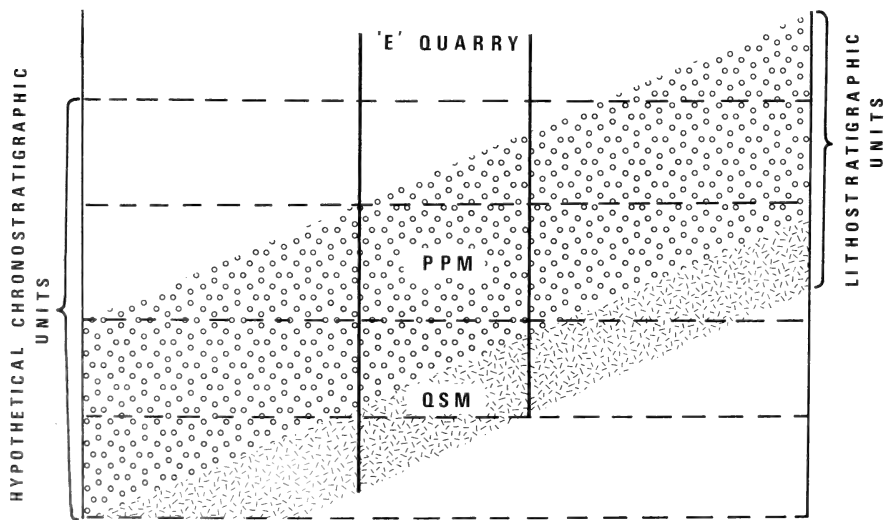


Fig. 8. A diagrammatic representation of the QSM and PPM lithostratigraphic units ('magnafacies'), and their relationship to hypothetical chronostratigraphic units ('parvafacies').

The PPM

The channel deposits, and incorporated fossil assemblages, of beds 3aS and 3aN of the PPM are essentially similar. However, bed 3aS was in the form of a relatively straight channel superimposed on an unconsolidated substratum, whereas in the bed 3aN area an outcrop of phosphatic rock caused a southward deflection in the course of the river, and, at least in flood times, it provided a consolidated substratum for part of the channel (Hendey 1980: 58–62, fig. 26). In addition, the seaward end of bed 3aS was truncated by the bed 3aN channel. (Fig. 6), which resulted in the loss from bed 3aS of the marsh and pond facies evident in bed 3aN (Table 3).

The bed 3aN deposits were recently discussed in some detail (Hendey 1980: 58–67), and were also mentioned earlier (Hendey 1976a: 228–230). The latter account also deals with bed 3aS, while this bed (formerly 3a) was also discussed by Hendey (1974a: 33, 36–37, 353).

While beds 3aS and 3aN have many species in common with the QSM, their faunas are also in some respects distinct (see pp. 45–53), and the condition of specimens and relative numbers of individuals in any given taxon may be very different. The most characteristic of the beds 3aS and 3aN taxa are the seal (*Homiphoca capensis*), giraffids (*Giraffa* sp., *Sivatherium hendeyi*), alcelaphine antelope (*Damalacra neanica* and *D. acalla*), and a reduncine (*Kobus subdolus*). There are, however, differences in the relative numbers of individuals represented in beds 3aS and 3aN, and to a lesser extent also in the taxa represented. For example, the alcelaphines occur much more commonly than giraffids in bed 3aS, whereas in bed 3aN the reverse applies. In addition, species of *Palaeotragus*, *Tragelaphus*, and *Kobus* are known only from bed 3aN.

Most of the fossils from beds 3aS and 3aN represent the remains of animals washed into the area by the river, but at least some must represent animals that were resident locally. The latter include aquatic species such as the seal and fishes, while others might have lived on the river-banks. For example, hyaenas might have roamed the banks scavenging carcasses stranded there.

The river might have had an important effect on the composition of the bed 3aS assemblage. At the time that much of the latter was being deposited, the river was flowing over the unconsolidated and often highly fossiliferous deposits of the QSM. It is certain that at least some, and perhaps even a great many, QSM fossils were picked up by the river and redeposited in bed 3aS. Since such derived fossils might have suffered only minimal transport, they would not necessarily show obvious signs of reworking. There is little likelihood of a similarly serious complication with the bed 3aN assemblage (Hendey 1976a: 230).

Although the deposits and faunas of the QSM, bed 3aS, and bed 3aN differ, and despite the evidence that intervals of time elapsed between their deposition, there can be little doubt that they date from a relatively short period and represent repetitive depositional phases of a single geological episode. The period was long enough for evolutionary changes to take place in

taxa common to more than one level (see p. 24), and it is possible that the composition of the local fauna also changed during this time (see p. 86). However, most of the faunal differences, and all of the geological ones, can be ascribed to the exposure in various areas and levels of differing depositional environments within a major depositional system (i.e. an estuary and associated environments).

Fossils do occur in the PPM deposits overlying bed 3aN, but they are not common and probably represent the remains of animals occasionally washed into a marine littoral environment by currents emanating from the river mouth, which was progressively further from the 'E' Quarry area as the early Pliocene transgression advanced.

The upper levels of the PPM, and, indeed, all the undifferentiated parts of this unit, include marine microfossils such as foraminifera, fish teeth, and mollusc fragments (Tankard 1974a).

The record of deposition of the PPM in the Langebaanweg area is probably incomplete, since there was evidently truncation of the higher levels during the subsequent late Pliocene regression.

Mobilization of phosphate in the PPM and its redeposition into phosphatic rock horizons might have continued after deposition of the PPM itself ceased. There are several phosphatic rock horizons in the more northerly exposures of the PPM in 'E' Quarry and it is evident that they did not form contemporaneously (Dingle *et al.* 1979: 89). The one that affected distribution of bed 3aN was formed after the accumulation of the QSM and before deposition of bed 3aN, while others higher in the sequence were formed subsequently. A possibly significant feature of these horizons is that they occur only in the more northerly exposures of the PPM. The bulk of the PPM deposits, which are spread out south and south-west from 'E' Quarry, have at most thin lenses of phosphatic rock which are superficially very different in appearance. The more northerly phosphatic rock horizons cannot have formed in a deep-water continental shelf situation, which was suggested in the case of the middle Miocene phosphatic rock (see p. 20). The fact that they occur only on what was the landward side of the developing Varswater Formation, suggests the possibility that seasonal movement of the watertable in the phosphate-rich sediments might have led to precipitation of a phosphatic matrix in the zone of movement.

Deposition of pelletal phosphorite apparently ceased during a stage in the transgression when the Langebaanweg area was so deeply covered by the sea that conditions necessary for its formation were no longer being met (see Birch 1977, fig. 4).

The Anyskop marine deposits

It was previously assumed that all those deposits overlying the PPM in the vicinity of 'E' Quarry were deposited subaerially during the Quaternary (e.g. Hendey 1974a; Tankard 1974a; Bishop 1980). However, this apparently applies to only part of the overlying succession.

Although pelletal phosphorite continued to accumulate at higher elevations south-east of Langebaanweg (e.g. Elandsfontein—Rogers 1980) during the latter stages of the early Pliocene transgression (i.e. in the shallower water close to the river mouth and shoreline), in the immediate vicinity of Langebaanweg only non-phosphatic deposits were being laid down. This conclusion is based on a reassessment of the calcareous deposits making up the bulk of Anyskop, the hill immediately south of 'E' Quarry. These deposits have been included in the 'Langebaan Limestone' (Visser & Schoch 1973), which Tankard (1976) defined as a member of the Bredasdorp Formation. The 'Langebaan Limestone' is generally regarded as a composite 'of limestone types of . . . aeolian origin' (Tankard 1976: 114). The continued recognition of this lithostratigraphic unit is open to question, since it is evident that limestones and calcretes of different ages and origin are included in it. The Anyskop calcareous deposits are a case in point. The reinterpretation of these deposits which is outlined below is tentative, and, although it may well be modified in future studies, it is obvious that previous interpretations are incorrect.

Anyskop is a prominent feature in the Langebaanweg area, rising to an elevation of over 70 m, while the mean elevation in the immediate vicinity is probably about 30 m. Deposits on its northern slope have been exposed by overburden stripping associated with the 'E' Quarry mining operation. Features of these deposits, including a previously unknown fossil content, have been revealed by three years (1977–1980) of subaerial weathering and erosion which took place while mining operations were suspended. The hill itself is a curious feature, since it may be the only one in a wide area around Langebaanweg which does not have a core of Cape granite. In fact, the bedrock beneath the hill is at about 35 m below sea-level (Rogers 1980), a situation which apparently applies within a radius of several kilometres. The existence of the hill, therefore, has no direct connection with the solid geology of the area.

Also anomalous is the fossil content of the calcareous deposits comprising much of Anyskop. According to Tankard (1974a: 280–281), foraminifera are abundant, with *Anomalina* tests outnumbering those of *Elphidium* 5 : 1, the former being 'essentially fresh', while the latter are weathered. Tankard's belief that the forams were 'blown inland subsequent to the regression of the sea responsible for the Varswater Formation' is inconsistent with the condition of the *Anomalina* tests and the fact that this genus occurs most commonly in continental shelf rather than beach situations (R. A. Martin, pers. comm.). It is much more likely that the fresh *Anomalina* specimens were deposited in a marine environment where no abrasion by wind or wave action was possible. On the other hand, *Elphidium* is common in inshore situations and the abraded conditions of the Anyskop specimens suggest that they might have been exposed to the wind or waves. It is probably also significant that, whereas *Elphidium* and other inshore forams are recorded from the underlying marine littoral PPM, *Anomalina* is not.

One possible interpretation of the above observations is that the calcareous

deposits of Anyskop were in part accumulated in a marine environment of deeper water than the PPM, and also in part on a beach or adjacent terrestrial environment. This is a combination of circumstances which exists on a submerged barrier or barrier island. It is perhaps significant that the south-east to north-west trend of Anyskop parallels at least a part of the sand-bar which existed in QSM and PPM times, and it is conceivable that a submerged barrier or barrier island was a vertical and north-eastward development from this sand-bar as the Pliocene transgression progressed. Figure 9 illustrates the hypothetical submerged barrier or barrier island in a 'drumstick' form of the kind described for such features by Hayes (1976). The most substantial part of this 'drumstick' survives as Anyskop today. The east-west trend of the barrier (Fig. 9) is conjectural, and it might instead have extended southwards towards Karnberg (Fig. 2; see also p. 39).

The development of this barrier was a very significant event, since the deposits constituting it were subsequently to protect from erosion the underlying and northward-extending Varswater Formation that survives today. The preservation of so substantial a body of unconsolidated late Tertiary sediment has hitherto been difficult to explain, just as there was no obvious reason why Anyskop should have been developed by aeolian action in its present position and form.

An apparent anomaly with this interpretation is the observation by Tankard (1974a) that the most commonly occurring fossils in the calcareous sands are shells of the land snail, *Trigonephrus globulus*. Also common are shells of

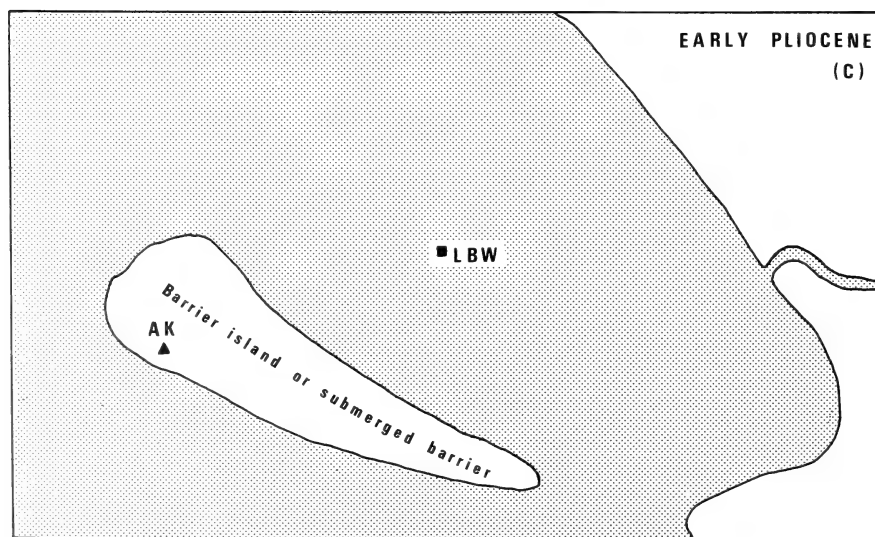


Fig. 9. The Langebaanweg area during the early Pliocene (sea-level cycle TP1). C. Period of deposition of the Anyskop marine deposits. Sea-level at about 60 m above present level (transgression maximum at 90 m). (See Fig. 4 for key.)

another, unidentified land snail. The snail shells are now known to occur together with fragmentary vertebrate remains, mainly of terrestrial species, although marine and freshwater taxa are also recorded. Associated with these fossils are 'fossil roots' (rhizoconcretions) and as yet unexplained circular structures of calcrete with infillings of reddish sands (Fig. 10). The latter have been suggested to represent remnants of tree stumps or clumps of sedge, termitaria, or solution cavities.

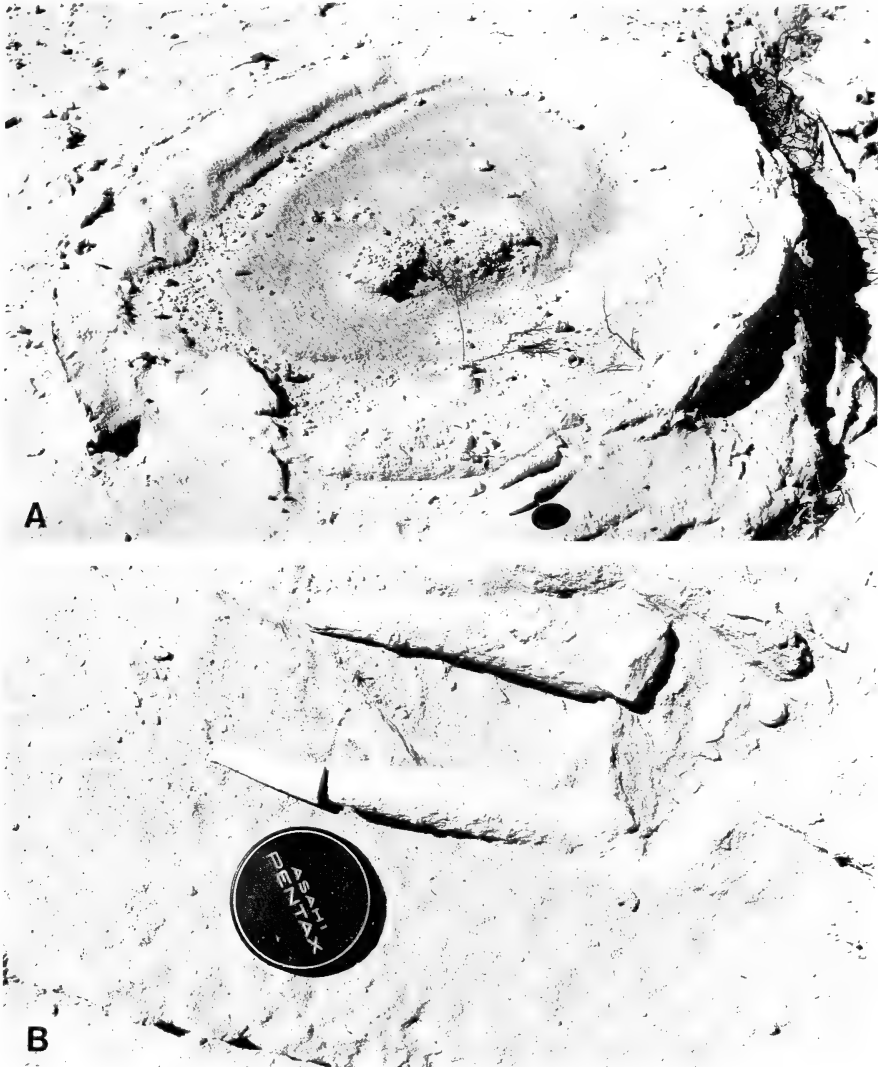


Fig. 10. A. An exposure of the Anyskop terrestrial deposits showing one of the unidentified features referred to in the text, together with snail shells and the horn-cores of an unidentified antelope. B. A close-up view of a snail shell and the antelope horn-cores.

There can be little doubt that these structures, the rhizoconcretions, and the fossils mark an old land surface. They appear to be confined to a horizon extending from high up the north slope of Anyskop down towards the 'E' Quarry exposures of the PPM, although they are not known to occur *in situ* below an elevation of about 40–45 m. In areas on the north slope which have been excavated well below the present surface, the structures and fossils are absent. These observations suggest that the old land surface was more or less coincident with the present northern contours of Anyskop, occurring over a limited vertical extent of the calcareous deposits immediately beneath the unconsolidated surface sands. In other words, the fossils were deposited *on* Anyskop at a time when the north slope was more or less in its present form.

The vertebrate fossil assemblage is as yet unstudied, and it may be too small and the fossils too fragmentary to give an accurate indication of age. The assemblage is, however, definitely distinct from those of the underlying QSM and PPM. It includes at least one species otherwise known only from the late Pliocene/early Pleistocene Baard's Quarry assemblage (i.e. *Hipparion baardi*, an advanced member of the lineage which includes the 'E' Quarry *H. cf. baardi*—Hooijer 1976; Hendey 1978a). On the other hand, an unidentified antelope from the Anyskop fauna (Fig. 10) is clearly distinct from the ones represented at Baard's Quarry, and, indeed, all other antelopes hitherto recorded from the south-western Cape.

The implications of the Anyskop ancient land surface will be discussed below, but its significance here is that there appears to be no direct association between its terrestrial fossils and the marine fauna (including forams) recorded by Tankard (1974a). Consequently, a distinction is made between the 'Anyskop marine deposits' and the 'Anyskop terrestrial deposits', with the former being correlated with the early Pliocene transgression, and the latter post-dating this event. There is an as yet undetermined relationship between the Anyskop deposits and those overlying the Varswater Formation on the western side of 'E' Quarry (exposure 1 of Dingle *et al.* 1979, figs 2–3).

The early Pliocene transgression reached an elevation of 90 m, which is about 20 m above the maximum height of Anyskop. While it is possible that post-early Pliocene erosion reduced the height of Anyskop, it might never have been as high as 90 m, which means that at least during the latter stages of the transgression, Anyskop was probably in the form of a submerged barrier rather than a barrier island.

Remnants of the 90 m marine platform exist to the south-east of Langebaanweg. Its presence is inferred from the topography (Mabbutt 1956), while marine deposits up to an elevation of 80 m have been recorded on the farm Elandsfontein (Rogers 1980). Evidently it was developed in the lee of a series of hills formed by outcrops of Cape granite. The trend of these hills is from north-west to south-east, roughly parallel to the present coast. The hills are Karnberg (177 m), 12 km south-south-west of Langebaanweg, followed by Massenberg (161 m), Groot Swartberg (287 m), and Slangkop (258 m). Subse-

quent to its formation the 90 m platform was incised by the valley of the Sout River, a northward-flowing tributary of the Berg River (Fig. 2).

It was suggested above that the Anyskop barrier island may have extended southwards in the direction of Karnberg, rather than eastwards as indicated in Figure 9. If this was indeed the case, then Karnberg and the other hills in the series must have been influencing the local topography at an earlier stage during the early Pliocene transgression. The Anyskop barrier island might in fact, have been a longshore spit extending northwards from Karnberg.

This, and other, uncertainties relating to the later history of the early Pliocene transgression should be resolved by further investigation of relevant deposits in the Langebaanweg area.

The early Pliocene transgression which resulted in deposition of the QSM, PPM, the Anyskop marine deposits and other marine deposits south-east of Langebaanweg, represents sea-level cycle TP1 of supercycle Tf (Vail & Hardenbol 1979: fig. 8).

The late Pliocene regression and early Pleistocene transgression

The history of late Pliocene and early Pleistocene deposition in the Langebaanweg area is as yet not well documented, and inference played a large part in the interpretation outlined below, with the nature and likely age of the Anyskop terrestrial deposits and Baard's Quarry fluvial deposits being of particular significance in this interpretation.

It is unlikely that Anyskop was in its present form during the early stages of the late Pliocene regression. Had this been the case then it would have been in the form of an island a few kilometres off the emergent mainland. The fact that a vertebrate fauna, which is correlated with an early stage of the regression, left traces of its presence on the north slope of Anyskop when the sea was at an elevation of between 40 and 60 m, means that a connection with the mainland must have existed. This connection probably followed the trend of the pre-existing coastal barrier, which might have been north-south, rather than east-west, as indicated in Figure 11.

Figure 11 also shows the ancient Berg River passing westwards along the northern side of this connection and meeting the sea to the south-west of 'E' Quarry. There is, in fact, no direct evidence for the position of the river, while its local presence is inferred simply because it is the most likely source of fresh water required by species such as the hippopotamus in the Anyskop fauna. A more tenuous indication that the river was present locally is the unequivocal evidence for its presence both during the early Pliocene (see above) and subsequently during the late Pliocene/early Pleistocene (see below).

A sea-level elevation of about 50 m at this time is deduced from the presence of a marine element in the Anyskop fauna, and from the recorded elevation of the Anyskop terrestrial fossils and associated features. In addition, the PPM of the Varswater Formation has been eroded down to a maximum elevation of 50–55 m in the vicinity of Anyskop. The maximum elevations for

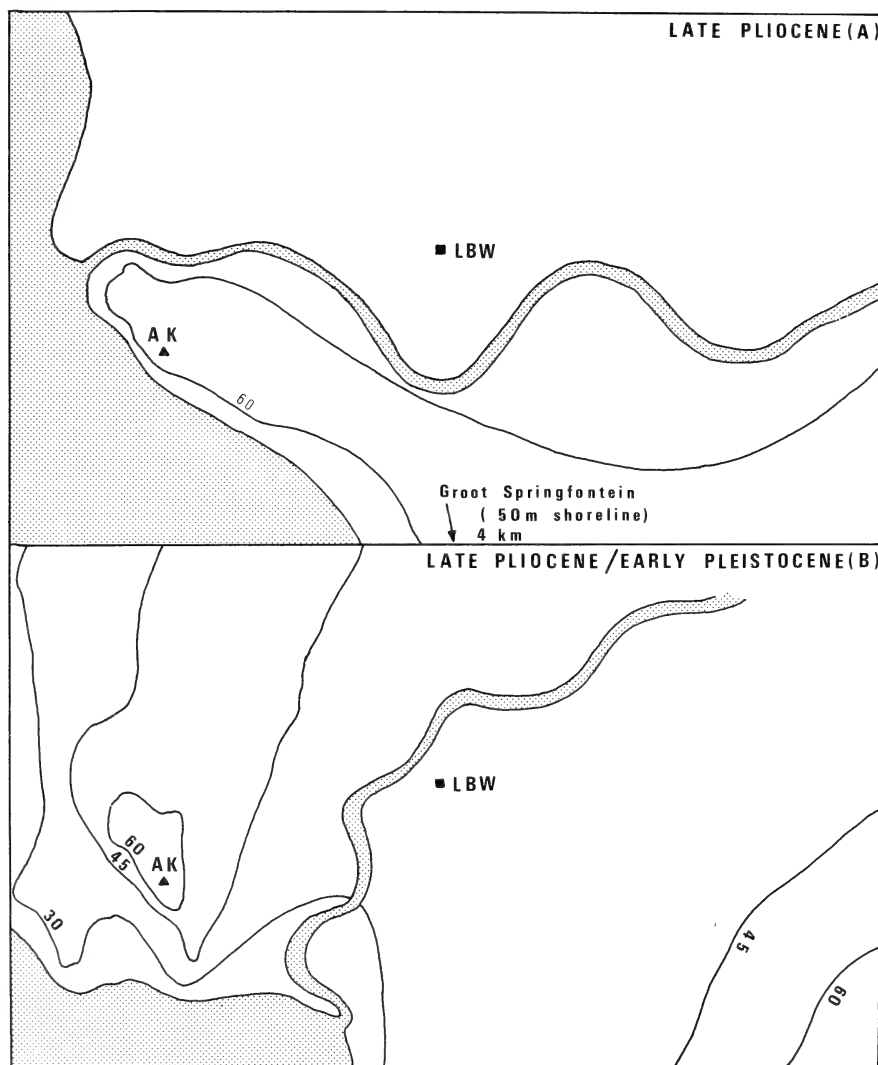


Fig. 11. The Langebaanweg area during the late Pliocene (sea-level cycle TP2) and the late Pliocene or early Pleistocene (sea-level cycle TP3 or Q1). A. Period of deposition of the Anyskop terrestrial deposits. B. Period of deposition of the Baard's Quarry fluvial deposits. (See Fig. 4 for key.)

the PPM recorded by Tankard (1974a) are 53–54 m near 'E' Quarry, 54 m on the farm Witteklip and at Paternoster, and 47–50 m at Duiker Eiland. Tankard also records a marine horizon at 50 m on the farm Groot Springfontein, south-east of Anyskop, the nature of the deposits and associated fossils indicating a shoreline situation.

The various occurrences at about 50 m elevation are here interpreted as representing a temporary stillstand in the Pliocene regression, probably the first of two such stillstands during this event recorded by Vail & Hardenbol (1979) in their synthesis of global sea-level changes (i.e. cycle TP2 of supercycle Tf).

Slender though the evidence may be, the vertebrate fauna of the Anyskop terrestrial deposits suggests an age close to, but not necessarily contemporaneous with, the fauna from the Baard's Quarry fluvatile deposits (i.e. late Pliocene/early Pleistocene). It is, therefore, not inconsistent with the inferred Pliocene age of the 50 m shoreline.

As indicated above, there is unequivocal evidence for the presence of the river during the late Pliocene/early Pleistocene. This is in the form of channel deposits revealed west of Langebaanweg station by the prospecting for, and mining of, phosphate (Tankard 1974a; Hendey 1978a). They are here referred to as the 'Baard's Quarry fluvatile deposits', and are correlated with the west coast 20 m shoreline. This represents either the second of the stillstands in the Pliocene regression recorded by Vail & Hardenbol (1979) (i.e. cycle TP3 of supercycle Tf), or the climax of the early Pleistocene transgression (i.e. cycle Q1 of supercycle Q).

According to Vail & Hardenbol (1979, fig. 8) cycle TP3 spanned the period between 3,8 and 2,8 Ma, the latter being taken by them as the Pliocene–Pleistocene boundary, while cycle Q1 is dated between 2,8 and 1,7 Ma. The mammalian fauna of the Baard's Quarry fluvatile deposits (= 'lower levels' fauna of Hendey 1978a) also suggested an age close to the Pliocene–Pleistocene boundary, and it has recently become evident that at least one element in this fauna is unlikely to be older than 1,9 Ma (see p. 95). Consequently, the Baard's Quarry fluvatile deposits are more likely to date from cycle Q1 than cycle TP3. This is consistent with the record of the cold-water fauna associated with the counterpart of the Baard's Quarry fluvatile deposits on the Namaqualand coast (Table 2; see also p. 16), and the suggestion that cold-water faunas are characteristic of the Quaternary.

Figure 11 shows the river meeting the sea south-east of Anyskop, with the pre-existing barrier island link to the mainland having been severed. If this link did exist, then it is most likely to have been destroyed by river erosion. The coincidence of this event with the 20 m stillstand is suggested by the fact that the Baard's Quarry fluvatile deposits are situated on a broad, flat plain (? an ancient floodplain), which extends southwards through the area where the hypothetical Anyskop–'mainland' connection existed (Fig. 11). It would have been at this time that Anyskop took on its present form.

Subsequently, the river underwent a radical change in direction in its lower course, shifting northwards to begin incising its present valley in the direction of St Helena Bay. This process continued during the Pleistocene and at least by the beginning of the late Pleistocene the Berg River must have been more or less in its present position, since Tankard (1976) has identified last interglacial marine deposits in the existing valley.

Once the river and the sea were no longer in the vicinity of Langebaanweg, sedimentation in the area was insignificant. The minor events of the Quaternary included the development of the unconsolidated aeolian sands which blanket the area, and duricrust (mainly calcrete) formation within them and in underlying deposits. Early Stone Age artefacts, probably of middle Pleistocene age, have been found cemented into the calcrete immediately underlying the surface sands on Anyskop, and there is evidence for post-middle Pleistocene human occupations in the area as well. There are recorded vertebrate fossil occurrences dating from the ?early Pleistocene (Skurwerug, near Saldanha), middle Pleistocene (Elandsfontein), and late Pleistocene (Sea Harvest at Saldanha, and others).

The late Cenozoic sequence in the Langebaanweg area is in many respects unique, and although much attention has been focused on it, especially during the last decade, most of the geological studies (e.g. Butzer 1973; Visser & Schoch 1973; Tankard 1974a; Bishop 1980) have dealt only superficially with the fossil occurrences and the nature of the various depositional environments represented. Consequently, there is still a need for further study directed specifically at the context of the recorded fossil assemblages and the history of the deposits, especially those post-dating the PPM of the Varswater Formation. Since large volumes of deposit have been mined away, it is no longer possible to retrieve all the information on the succession which was once available. Nevertheless, documentary records, sediment samples and exposures still exist, and they offer a potential for further research.

BIOLOGY

FLORA

The flora of the Langebaanweg area during the period of deposition of the late Cenozoic succession is not well known. Initially only indirect evidence was available from which the nature of the local vegetation during QSM and PPM times could be deduced. For example, large browsers amongst the herbivores, particularly the long-necked giraffe (*Giraffa* sp.), have been cited on several occasions as indicating the presence of trees (e.g. Hendey 1973, 1974a, 1976a, 1980). On the other hand, hypsodont grazing species such as the rhinoceros (*Ceratotherium praecox*) indicate that grasslands were also present. The possible significance of the relative abundance of browsers and grazers at different levels within the Varswater Formation will be discussed later (see p. 75).

Other indirect evidence for the presence of plants was that of leaf impressions, probably of grass or reeds, on coprolites from the QSM (Hendey 1976a: 224). Attempts to recover pollens from coprolites have so far proved fruitless.

Physical remains of plants themselves are limited to pollens, algal nuckles, and fragments of petrified roots. Studies on pollens from the 'peats' of the Varswater Formation and underlying deposits have yet to be published, but passing references to these pollens have been made by Tankard (1975b), Hendey (1976a), Tankard & Rogers (1978), and Dingle *et al.* (1979). In

addition, although not specifically mentioned, the pollens contributed to Coetzee's (1978) study on vegetational changes in the south-western Cape during the late Tertiary. These pollens indicate that the local vegetation during pre-GM times (i.e. Miocene) was dominated by forests and woodlands, whereas by QSM times (i.e. early Pliocene) sclerophyll (fynbos) vegetation was becoming prominent. Details of the Langebaanweg pollen record will be published elsewhere (J. A. Coetzee, in preparation).

The algal nucules (charophytes) were identified and discussed by Kensley (1977), and they have also been studied by I. Soulié (Montpellier), although her report on them is as yet unpublished. They were preserved in the tidal flat bed of the QSM (i.e. QSM III), and were probably derived from freshwater ponds on the QSM floodplain (i.e. QSM I). The existence of such ponds was postulated by Hendey (1976a).

The fossil roots, which are in the form of slender fragments mostly from the QSM, have not been studied. It is unlikely that they will reveal much about the plants to which they belonged.

In conclusion, it should be mentioned that the rhizoconcretions and the unidentified structures of the Anyskop terrestrial deposits may provide some indication of the local vegetation later in the Pliocene.

FAUNA

Composition

This section deals only with the fauna of the Varswater Formation, from which the assemblage of invertebrate and vertebrate fossils is exceptionally large, both in terms of the numbers of specimens and in the variety of species represented. However, it represents only a small fraction of the material which was preserved in the deposits, much of which was lost during mining operations and much of which remains unexcavated.

At least 230 distinct taxa have been recognized, ranging from protozoans to mammals. Vertebrates predominate, and there are many phyla of lower animals that are not recorded. Important groups such as the insects are also lacking, the only tangible evidence of their presence being grooves on bovid horn-cores left by keratophagous insect larvae (Fig. 12). Most specimens are well preserved and individual species assemblages range from a few to many thousands of specimens. Most taxa are identifiable to species level, and incomplete identifications usually indicate that taxonomic studies have yet to be undertaken.

The list of taxa which follows is given in systematic order and according to the horizon from which material was derived. Material of doubtful provenance (?) is listed under horizons where its presence was likely. In the case of the equid, *Hipparion* cf. *namaquense*, it is still not known if the relevant material came from the uppermost levels of the PPM, or the lowermost levels of the overlying deposits (Hooijer 1976). Inferred habitat preferences are given, and in instances where resting and feeding habitats differ (e.g. amongst many birds), the latter are recorded.

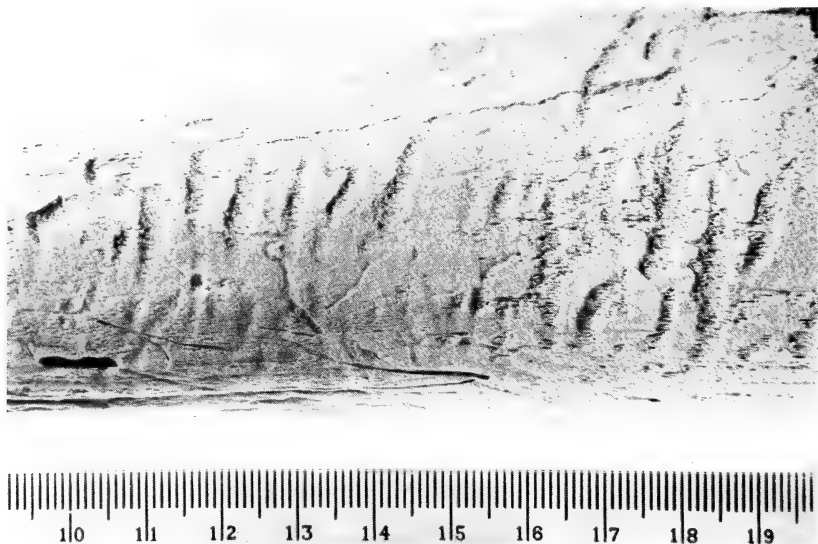


Fig 12. Marks left on a *Mesembriportax acrae* horn-core from the PPM 3aS (SAM-PQ-40071) by keratophagous insect larvae.

Although the lists for individual horizons broadly reflect the local fauna of the period of deposition, they do not necessarily represent the fauna of a single habitat. In the case of some levels it is possible that the assemblages include specimens derived from pre-existing deposits. This applies particularly in the case of the fluvialite deposits (beds 3aS and 3aN), which are, in addition, comprised largely of taxa whose remains were washed into the area from upstream habitats. Palaeoecological interpretations of the assemblages constituting the 'E' Quarry fauna must, therefore, take these factors into account.

An example of the palaeoecological studies which are possible is that by Kensley (1977) on the invertebrate assemblage from QSM III (i.e. the tidal-flat bed). In this instance the remains of the resident animal community were supplemented by others washed downstream by the river and upstream by the tides. This assemblage proved to be essentially similar to ones in comparable situations today, and, interestingly, it proved a better indication of the nature of the depositional environment than the sediments themselves.

This was a general rule with most 'E' Quarry sediments, and attempts to interpret their history without taking into account the composition of individual assemblages and the condition of specimens, resulted in mistaken conclusions. For example, Butzer (1973) misinterpreted the depositional environments of the QSM (= Bed 2) and bed 3aS (= bed 3a) through using only geological evidence. While Bishop (1980) evidently appreciated the significance of the fossils, he supported Butzer's conclusions and ignored the palaeontological evidence which became available after 1970.

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference	
PHYLUM PROTOZOA							
ORDER FORAMINIFERA							
<i>Ammonia beccarii</i>	.	.	—	—	×	} marine (littoral) and estuarine marine (littoral; attached to vegetation etc.)	
<i>Elphidium advenum</i>	.	.	—	—	×		
<i>Cibicides lobatulus</i>	.	.	—	—	×		
<i>Planorbulina mediterraneensis</i>	—	—	—	—	×		
<i>Rosalina</i> cf. <i>bradyi</i>	.	.	—	—	×		
PHYLUM BRACHIOPODA (lamp shells)							
<i>Kraussina rubra</i>	.	.	×	—	—	marine (rocky shore)	
PHYLUM ECHINODERMATA							
CLASS ECHINOIDEA (sea urchins)							
<i>Parechinus angulosus</i>	.	.	×	—	—	marine (rocky shore)	
PHYLUM ARTHROPODA							
CLASS CRUSTACEA							
ORDER CIRRIPIEDIA (acorn barnacles)							
Gen. and sp. indet.	.	×	—	—	—	marine (rocky shore)	
? ORDER DECAPODA (lobsters etc.)							
Gen. and sp. indet.	.	×	—	—	—	marine, estuarine and fresh water	
SUBCLASS OSTRACODA							
Family Cytheridae							
<i>Gomphocythere expansa</i>	.	.	×	—	—	} fresh water	
Family Cyprididae							
<i>Zonocypris cordata</i>	.	.	×	—	—		
Family not det.							
Gen. and at least 3 spp not det.	—	×	—	—	—		
PHYLUM MOLLUSCA							
CLASS GASTROPODA							
ORDER ARCHAEOGASTROPODA							
Family Patellidae (limpets)							
<i>Cellana capensis</i>	.	.	×	—	—	marine (rocky shore, warm water)	
? <i>Cellana</i> sp.	.	.	×	—	—	} marine (rocky shore)	
<i>Patella granularis</i>	.	.	×	—	—		
Family Fissurellidae (keyhole limpets)							
<i>Diodora parviforata</i>	.	.	×	—	—	marine (rocky shore)	
Family Haliotidae (perlemoens or abalones)							
* <i>Haliotis saldanhae</i>	.	.	×	—	—	} marine (rocky shore)	
<i>Haliotis</i> sp.	.	.	×	—	—		
Family Trochidae (top shells)							
<i>Oxystele tigrina</i>	.	.	×	—	—	} marine (rocky shore)	
<i>Oxystele variegata</i>	.	.	—	×	—		
<i>Gibbula benzi</i>	.	.	—	×	—		
Family Turbinidae (turban shells)							
<i>Turbo sarmaticus</i>	.	.	×	—	—	marine (rocky shore, warm water)	
Family Phasianellidae (pheasant shells)							
<i>Tricolia neritina</i>	.	.	×	×	—	marine (rocky shore)	
<i>Tricolia capensis</i>	.	.	—	×	—	marine (rocky shore, cold water)	
ORDER MESOGASTROPODA							
Family Littorinidae (periwinkles)							
<i>Littorina</i> cf. <i>knysnaensis</i>	.	—	×	—	—	} marine (rocky shore)	
? <i>Littorina</i> sp.	.	×	—	—	—		

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
Family Hydrobiidae (snails)						
<i>Tomichia ventricosa</i>	.	×	—	—	—	fresh or brack water
Family Assimineidae (snails)						
<i>Assiminea</i> sp.	.	×	—	—	—	mainly estuarine
ORDER NEOGASTROPODA						
Family Muricidae (rock shells or whelks)						
<i>Ocenebra scrobiculata</i>	.	×	—	—	—	marine (rocky shore)
Family Thaisidae (rock shells or whelks)						
<i>Thais dubia</i>	.	×	—	—	—	marine (rocky shore)
Family Columbellidae (dove shells)						
<i>Pyrene albuginosa</i>	.	×	—	—	—	marine (rocky shore, warm water)
Family Nassariidae (plough shells, dog whelks)						
<i>Bullia</i> sp.	.	×	—	—	—	marine and/or estuarine
<i>Bullia digitalis</i>	.	×	—	—	—	marine (sandy shore)
<i>Bullia laevisissima</i>	.	×	—	—	—	marine (sandy shore) and estuarine
<i>Bullia</i> sp. nov.	.	×	—	—	—	marine and/or estuarine
<i>Nassarius</i> cf. <i>analogicus</i>	.	×	—	—	—	marine (sandy shore) and estuarine
<i>Nassarius</i> sp. B	.	×	—	—	—	marine and/or estuarine
<i>Nassarius</i> sp. C	.	×	—	—	—	marine and/or estuarine
Family Marginellidae						
<i>Marginella</i> sp.	.	×	—	—	—	marine and/or estuarine
Family Turridae (screw shells)						
' <i>Crassispira</i> ' sp.	.	×	—	—	—	} marine
' <i>Clavatula</i> ' sp.	.	×	—	—	—	
' <i>Turris</i> ' sp.	.	×	—	—	—	
ORDER ENTOMOTAENIATA						
Family Pyramidellidae						
<i>Turbonilla kraussi</i>	.	×	—	—	—	} marine
? <i>Pyramidella</i> sp.	.	×	—	—	—	
ORDER BASOMMATOPHORA						
Family Siphonariidae (false limpets)						
<i>Siphonaria</i> sp.	.	×	—	—	—	marine (rocky shore)
Family Ferrissidae (snails)						
<i>Burnupia capensis</i>	.	×	—	—	—	on rushes in fresh water or estuaries
Family Planorbidae (snails)						
<i>Ceratophallus natalensis</i>	.	×	—	—	—	fresh water (sub- tropical, tropical)
<i>Bulinus</i> ' <i>tropicus</i> '	.	×	—	—	—	fresh water
ORDER STYLOMMATOPHORA						
Family Succineidae (snails)						
<i>Succinea</i> sp.	.	×	—	—	—	terrestrial or semi- aquatic (fresh water)
Family Endodontidae (snails)						
<i>Trachycystis</i> cf. <i>capensis</i>	.	×	—	—	—	terrestrial

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference	
CLASS AMPHINEURA							
Family Chitonidae (chitons)							
<i>Chiton nigrovirescens</i>	.	—	×	—	—	marine (rocky shore, cold water)	
CLASS PELECYPODA							
Family Donacidae (sand mussels)							
<i>Donax serra</i>	.	cf.	×	—	—	} marine (sandy shore)	
<i>Donax</i> sp(p)	.	×	—	—	—		
Family Carditidae (false cockles)							
* <i>Cuna aquaedulcensis</i>	.	—	×	—	—	marine	
Family Arcidae (ark shells)							
<i>Barbatia obliquata</i>	.	×	—	—	—	marine (rocky shore, warm water)	
Family Mytilidae (mussels)							
? <i>Perna</i> sp.	.	×	—	—	—	marine (rocky shore)	
Family Veneridae (venus shells)							
<i>Pitar</i> sp.	.	×	—	—	—	marine	
MOLLUSCA INDET.	.	—	—	—	×		
PHYLUM CHORDATA							
CLASS CHONDRICHTHYES							
ORDER SELACHII (sharks)							
Family Hexanchidae							
<i>Notidanus serratissimus</i>	.	×	—	—	—	marine	
Family Carcharhinidae							
<i>Carcharhinus melanopterus</i>	.	×	—	—	—	} marine (warm water)	
<i>Carcharhinus limbatus</i>	.	×	—	—	—		
<i>Galaeorhinus</i> sp.	.	×	—	—	—		
<i>Prionace glauca</i>	.	×	—	—	—		
<i>Negaprion</i> or <i>Hypoprion</i> sp.	.	×	—	—	—		
Family Odontaspidae							
<i>Odontaspis accutissima</i>	.	×	—	—	—	} marine	
<i>Odontaspis</i> sp. B	.	×	—	—	—		
<i>Odontaspis</i> sp. C	.	×	—	—	—		
Family Otodontidae							
<i>Megaselachus megalodon</i>	.	×	—	—	—	} marine	
Family Carcharodontidae							
<i>Carcharodon</i> sp.	.	×	—	—	—		
Family Isuridae							
<i>Isurus</i> sp.	.	×	—	—	—	} marine (warm water)	
Family Squalidae							
<i>Squalus</i> sp.	.	×	—	—	—		
Family Squatinaidae							
<i>Squatina africana</i>	.	×	—	—	—	marine (warm water)	
<i>Squatina</i> sp. B	.	×	—	—	—	marine	
SELACHII not det.	.	×	×	×	—		
ORDER BATOIDEA (skates, rays)							
Family Rajidae (skates)							
<i>Raja</i> sp.	.	×	—	—	—	} marine	
Family Trygonidae (sting rays)							
Gen. and sp. not det.	.	×	—	—	—		
Family Myliobatidae (eagle rays)							
<i>Myliobatis</i> sp.	.	×	—	—	—	} marine	
CLASS OSTEICHTHYES							
ORDER PERCIFORMES							
Family Sparidae (mussel-crackers)							
Gen. and sp. not det.	.	×	—	—	—	marine	

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
ORDER SILURIFORMES						
Family Tachysuridae (catfish)						
? <i>Tachysurus</i> sp.	.	—	×	×	—	marine and estuarine
OSTEICHTHYES not det.	.	×	×	×	×	
CLASS AMPHIBIA						
ORDER ANURA (frogs, toads)						
Gen. and sp(p) not det.	.	—	×	×	—	terrestrial and fresh water
CLASS REPTILIA						
ORDER CHELONIA (tortoises, turtles)						
<i>Chersina</i> sp.	.	×	×	×	—	terrestrial
Gen. and sp. not det.	.	—	—	—	—	marine or fresh water
Gen. and sp. not det.	.	—	—	×	—	marine or fresh water
ORDER SQUAMATA						
SUBORDER LACERTILIA						
Family Chameleontidae (chameleons)						
Gen. and sp(p) not det.	.	—	×	×	—	bushes and trees
Family Gekkonidae (geckos)	.					
Gen. and sp(p) not det.	.	—	×	×	—	terrestrial
Family Varanidae (leguans, monitor lizards)						
<i>Varanus</i> sp.	.	—	×	—	—	terrestrial or fresh water
SUBORDER OPHIDIA (snakes)						
Gen. and sp(p) not det.	.	—	×	×	—	terrestrial
SQUAMATA not det.	.	—	×	×	—	
CLASS AVES						
ORDER STRUTHIONIFORMES						
Family Struthionidae (ostriches)						
<i>Struthio</i> sp.	.	—	×	×	—	terrestrial (open country)
ORDER SPHENISCIFORMES						
Family Spheniscidae (penguins)						
** <i>Inguza predemersus</i>	.	—	×	cf.	?	} marine (mainly coastal, cold water)
** <i>Dege hendeyi</i>	.	cf.	×	?	×	
ORDER PODICIPEDIFORMES						
Family Podicipedidae (grebes)						
Gen. and sp. not det.	.	—	×	—	—	? fresh water
ORDER PROCELLARIIFORMES (petrels etc.)						
Gen. and at least 3 spp not det.	.	—	×	—	—	marine (pelagic)
ORDER PELECANIFORMES (pelicans etc.)						
Fam., gen. and sp. not det.	.	—	×	—	—	
Family Phalacrocoracidae (cormorants)						
Gen. and at least 2 spp not det.	.	—	×	—	—	marine and/or fresh water
? Family Sulidae (gannets)						
Gen. and sp. not det.	.	—	×	—	—	marine
ORDER CICONIIFORMES						
Family Ciconidae (storks)						
Gen. and sp. not det.	.	—	×	—	—	terrestrial (open country and/or marsh)

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
Family Threskiornithidae (ibises, spoonbills)						
Gen. and sp. not det.	—	×	—	—	—	terrestrial (open country) and fresh water
ORDER ANSERIFORMES						
Family Anatidae (ducks, geese)						
Gen. and at least 4 spp not det.	—	×	—	×	—	fresh water and estuarine
ORDER FALCONIFORMES						
Family Falconidae (falcons)						
Gen. and sp. not det.	—	×	—	—	—	aerial, arboreal and/or terrestrial
Family Accipitridae (hawks, eagles etc.)						
Gen. and at least 4 spp not det.	—	×	—	×	—	aerial, arboreal and/or terrestrial
? Gypaetinae (vultures) gen. and sp. not det.	—	×	—	—	—	terrestrial (open country)
ORDER GALLIFORMES						
Family Phasianidae (game birds)						
Gen. and at least 2 spp (francolin and quail) not det.	—	×	×	×	—	terrestrial (open country with low cover)
ORDER GRUIFORMES						
Family Gruidae (cranes)						
Gen. and sp. not det.	—	—	—	×	—	terrestrial (open country, marsh)
Family Rallidae (rails)						
Gen. and sp. not det.	—	×	—	×	—	terrestrial (dense cover) and fresh water
Family Otidae (bustards)	—	×	—	—	—	terrestrial (open, mainly dry country)
ORDER CHARADRIIFORMES (shorebirds)						
Fam., gen. and at least 10 spp not det.	—	×	—	×	—	fresh water, estuarine and/or marine
Family Pteroclididae (sandgrouse)						
Gen. and sp. not det.	—	×	—	—	—	terrestrial (near water)
ORDER COLUMBIFORMES						
Family Columbidae (pigeons, doves)						
Gen. and at least 2 spp not det.	—	×	—	×	—	terrestrial and arboreal
ORDER PSITTACIFORMES (parrots)						
Fam., gen. and at least 2 spp not det.	—	×	—	?	—	arboreal (forests, woodlands)
ORDER STRIGIFORMES						
Family Strigidae (owls)						
Gen. and at least 2 spp not det.	—	×	—	—	—	arboreal and terrestrial

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
ORDER COLIIFORMES						
Family Coliidae (colies)						
Gen. and sp. not det.	—	×	—	—	—	arboreal (bushland and woodland)
ORDER CORACIIFORMES (rollers etc.)						
Fam., gen. and sp. not det.	—	×	—	—	—	arboreal and terrestrial
? Family Alcedinidae (kingfishers)						
Gen. and at least 2 spp not det.	—	×	—	—	—	fresh water
ORDER PICIFORMES (woodpeckers etc.)						
Fam., gen. and at least 2 spp not det.	—	×	—	—	—	arboreal and terrestrial
ORDER APODIFORMES						
Family Apodidae (swifts)						
Gen. and sp. not det.	—	—	×	—	—	aerial
ORDER PASSERIFORMES (songbirds)						
Fam., gen. and at least 9 spp not det.	—	×	—	×	—	varied
AVES not det.	—	×	×	×	—	
CLASS MAMMALIA						
ORDER INSECTIVORA						
Family Chrysochloridae (golden moles)						
<i>Chrysochloris</i> sp.	—	×	×	×	—	fossorial
Family Soricidae (shrews)						
<i>Mysorex</i> sp.	—	×	—	—	—	} terrestrial
<i>Suncus</i> sp.	—	×	—	—	—	
Soricidae gen. and sp(p) not det.	—	×	×	×	—	
Family Macroscelididae (elephant shrews)						
<i>Elephantulus</i> sp.	—	×	×	×	—	
ORDER CHIROPTERA (bats)						
Family Vespertilionidae						
<i>Eptesicus</i> sp.	—	×	—	—	—	aerial
ORDER PRIMATES						
Family Cercopithecidae (monkeys etc.)						
Gen. and sp. indet.	—	×	—	—	—	arboreal and terrestrial
ORDER PHOLIDOTA (pangolins)						
<i>Phataginus</i> sp.	—	×	—	—	—	terrestrial
ORDER TUBULIDENTATA (aardvarks)						
Gen. and sp. not det.	—	×	—	×	—	terrestrial
ORDER CARNIVORA						
Family Canidae (foxes, jackals etc.)						
Gen. and sp. not det. (? aff. 'Canis' brevirostris)	—	—	×	?	—	} terrestrial
<i>Vulpes</i> sp. (fox)	—	—	×	×	—	
Family Ursidae (bears)						
* <i>Agriotherium africanum</i>	—	—	×	×	—	terrestrial (? woodlands)

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
Family Mustelidae (weasels, martens etc.)						
<i>Plesiogulo monspessulanus</i> (wolverine)	—	×	?	—	—	terrestrial (? woodlands)
* <i>Mellivora benfieldi</i> (honey badger)	—	—	×	×	—	terrestrial
<i>Enhydriodon africanus</i> (otter)	—	—	×	×	—	fresh water
Family Phocidae (seals)						
** <i>Homiphoca capensis</i>	cf.	×	×	×	—	marine and ? estuarine
Family Viverridae (mongooses etc.)						
' <i>Viverra</i> ' <i>leakeyi</i> (? aff. <i>Civettictis</i>) (civet)	—	×	—	×	—	} terrestrial
Viverrinae gen. and sp. not det. (? aff. <i>Pseudocivetta</i>) (civet)	—	×	×	×	—	
<i>Genetta</i> sp. (genet)	—	×	—	—	—	
<i>Herpestes</i> spp A, B (mongooses)	—	×	×	—	—	
Herpestinae spp C, D, E (mongooses)	—	×	—	—	—	
Herpestinae not det.	—	—	×	×	—	
Family Hyaenidae (hyaenas)						
* <i>Adcrocuta</i> <i>australis</i>	—	×	?	?	—	} terrestrial
* <i>Ictitherium preforfex</i>	—	—	×	×	—	
* <i>Hyaena abronia</i>	—	×	×	×	—	
<i>Hyaenictitherium namaquense</i>	—	×	—	—	—	
<i>Euryboas</i> sp.	—	×	×	×	—	
<i>Hyaenidae</i> sp. E	—	—	×	—	—	
<i>Hyaenidae</i> not det.	—	—	×	×	—	
Family Felidae (cats)						
' <i>Machairodus</i> ' sp. (sabre- tooth)	—	*×	—	—	—	} terrestrial
<i>Homotherium</i> sp. (sabre- tooth)	—	×	×	cf.	—	
<i>Felis</i> sp. (wildcat-like)	—	×	—	—	—	
<i>Felis</i> aff. <i>issiodorensis</i> (lynx- like)	—	×	×	×	—	
* <i>Felis obscura</i> (lynx-like)	—	—	×	—	—	
<i>Dinofelis diastemata</i> (false sabre-tooth)	—	×	×	×	—	
Felidae not det.	—	—	×	×	—	
CARNIVORA not det.						
Gen. and sp. not det. (Canidae or Viverridae)	—	×	—	—	—	
Gen. and sp. not det. (? Procyonidae)	—	×	—	—	—	
Gen. and sp. not det. (? Lutrinae)	—	×	—	—	—	
ORDER PROBOSCIDEA (elephants and kin)						
Family Gomphotheriidae						
<i>Anancus</i> sp.	—	×	×	—	—	} terrestrial (woodlands)
Family Elephantidae						
<i>Mammuthus subplanifrons</i>	—	×	?	×	—	

		GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
ORDER	HYRACOIDEA (hyraxes or dassies)						
Family	Procaviidae						
	<i>Procavia</i> cf. <i>antiqua</i> . . .	—	×	—	?	—	terrestrial or arboreal
ORDER	PERISSODACTYLA						
Family	Equidae (horses)						
	<i>Hipparion</i> cf. <i>primigenium</i> . . .	×	—	—	—	—	} terrestrial (grasslands)
	<i>Hipparion</i> cf. <i>baardi</i> . . .	—	×	×	×	—	
	<i>Hipparion</i> cf. <i>namaquense</i> . . .	—	—	—	—	?	
Family	Rhinocerotidae (rhinos)						
	<i>Ceratotherium praecox</i> . . .	—	×	×	—	—	}
ORDER	ARTIODACTYLA						
Family	Tayassuidae (peccaries)						
	* <i>Pecarichoerus</i> ? (or <i>Barberahyus</i>) <i>africanus</i> . . .	—	—	×	×	—	terrestrial
Family	Suidae (pigs)						
	<i>Nyanzachoerus</i> cf. <i>pattersoni</i> (or <i>kanamensis</i>) . . .	—	×	—	—	—	} terrestrial (? woodlands)
	<i>Nyanzachoerus</i> cf. <i>jaegeri</i> . . .	—	—	×	—	—	
Family	Hippopotamidae (hippos)						
	Gen. and sp. not det.	—	—	×	×	—	fresh water and terrestrial
Family	Giraffidae (giraffes)						
	* <i>Sivatherium hendeyi</i> . . .	—	×	×	×	—	} terrestrial (woodlands)
	<i>Palaeotragus</i> cf. <i>germaini</i> . . .	—	—	—	×	—	
	<i>Giraffa</i> sp.	—	×	×	×	—	
Family	Bovidae (buffaloes, antelopes etc.)						
	<i>Tragelaphus</i> sp. A (nyala-like)	—	×	×	×	—	} terrestrial (woodlands)
	<i>Tragelaphus</i> sp. B (nyala-like)	—	—	—	×	—	
	** <i>Mesembriportax</i> (or <i>Miotragocerus</i>) <i>acrae</i> (kudu like relative of nilgai) . . .	—	×	×	×	—	
	* <i>Simatherium demissum</i> (buffalo)	—	×	×	×	—	terrestrial (? grasslands)
	* <i>Kobus subdolos</i> (kob-like) . . .	—	—	×	×	—	} terrestrial (woodlands near fresh water)
	<i>Kobus</i> sp. B (kob-like) . . .	—	—	—	×	—	
	** <i>Damalacra neanica</i> (hartebeest-like) . . .	—	—	×	×	—	} terrestrial (grasslands)
	** <i>Damalacra acalla</i> (hartebeest-like)	—	×	×	×	—	
	* <i>Raphicerus paralius</i> (steenbok)	—	×	×	×	—	
	<i>Gazella</i> sp. (gazelle)	—	×	×	×	—	} terrestrial (? grasslands)
	Ovibovini gen. and at least 2 spp not det.	—	×	×	×	—	
ORDER	LAGOMORPHA						
Family	Leporidae (hares, rabbits)						
	<i>Pronalagus</i> sp.	—	×	×	×	—	terrestrial
ORDER	RODENTIA						
Family	Bathyergidae (rodent moles)						
	<i>Bathyergus</i> sp.	—	×	×	×	—	} fossorial
	<i>Cryptomys</i> sp.	—	×	—	?	—	
Family	Hystricidae (porcupines)						
	Gen. and sp. not det. A . . .	—	×	—	—	—	} terrestrial
	Gen. and sp. not det. B . . .	—	—	×	×	—	

	GM	QSM	PPM 3aS	PPM 3aN	PPM undiff.	Inferred habitat preference
Family Cricetidae (rats, mice, gerbils etc.)						
<i>Mystromys</i> sp. A . . .	—	×	—	—	—	} terrestrial
<i>Mystromys</i> cf. <i>darti</i> . . .	—	×	—	—	—	
<i>Mystromys</i> cf. <i>hausleitneri</i> . . .	—	×	—	—	—	
<i>Gerbillus</i> or <i>Desmodillus</i> sp. . . .	—	×	—	—	—	
<i>Dendromys</i> sp.	—	×	—	—	—	
<i>Steatomys</i> or <i>Malacothrix</i> sp. . . .	—	×	—	—	—	terrestrial (? woodlands)
Family Muridae (rats, mice)						
<i>Aethomys</i> spp A, B	—	×	—	—	—	} terrestrial
<i>Mus</i> spp A, B	—	×	—	—	—	
<i>Rhabdomys</i> sp.	—	×	—	—	—	
** <i>Euryotomys pelomyoides</i>	—	×	—	—	—	terrestrial (? near fresh water)
Family Muscardinidae (dormice)						
<i>Graphiurus</i> sp.	—	×	—	—	—	terrestrial (? woodlands)
RODENTIA not det.	—	×	×	×	—	
ORDER CETACEA (whales, dolphins)						
Gen. and spp not det.	×	×	×	×	—	marine
* sp. nov.						
** gen. et sp. nov.						

References:

- Foraminifera—Tankard 1975b.
 Other invertebrates—Kensley 1972, 1977; Tankard 1975b; unpublished.
 Chondrichthyes—Hulley, in Henley 1976a.
 Osteichthyes—unpublished.
 Amphibia/Reptilia—unpublished.
 Aves (Spheniscidae)—Simpson 1971, 1975, 1979.
 Aves (other)—Rich 1980; unpublished.
 Mammalia (Insectivora, Chiroptera, Lagomorpha, Rodentia—excluding Hystricidae)—Pocock 1976.
 Mammalia (Rodentia—Hystricidae)—unpublished.
 Mammalia (Primates, Pholidota, Tubulidentata, Hyracoidea, Hippopotamidae, Cetacea)—unpublished, but some details in Henley 1976a.
 Mammalia (Carnivora)—Henley 1972a, 1974a, 1974b, 1977, 1978c, 1978d, 1980; Henley & Repenning 1972; Wolff *et al.* 1973; De Muizon & Henley 1980.
 Mammalia (Proboscidea)—Maglio & Henley 1970; Maglio 1973; Coppens *et al.* 1978.
 Mammalia (Perissodactyla)—Hooijer 1972, 1976, 1978; Churcher & Richardson 1978; Henley 1978a.
 Mammalia (Tayassuidae)—Henley 1976b; Cooke & Wilkinson 1978.
 Mammalia (Suidae)—unpublished, but referred to by Cooke & Wilkinson 1978, and Harris & White 1979.
 Mammalia (Giraffidae)—Harris 1976; Churcher 1978; unpublished.
 Mammalia (Bovidae)—Gentry 1974, 1978, 1980.

The observations that follow supplement the last summary statement on the composition of the 'E' Quarry fauna (Henley 1976a: 231–243).

Most of the identified invertebrates are conspecific with, or closely related to, living forms and most have counterparts still living in the Langebaanweg area or adjacent ocean. Two new species have been recorded amongst the Mollusca. Marine forms predominate, but estuarine, freshwater and terrestrial

species are also recorded. Palaeoenvironmentally significant species will be discussed later (see p. 68).

Lower vertebrates (fish, amphibians and reptiles) are largely unstudied, although the cartilaginous fish (sharks, skates and rays) and the terrestrial tortoise (*Chersina* sp.) have received some expert attention. Other groups may well be more diverse than the preceding list indicates but, although available material is abundant, it is for the most part fragmentary and identification of taxa may be difficult. With the exception of some sharks (see p. 68), the lower vertebrates apparently represent forms which still occur in the region, or in the adjacent ocean.

The remains of birds are also abundant, a preliminary study having revealed that 'E' Quarry is the richest pre-Pleistocene fossil bird locality in the world (Rich 1980). Although bird remains are less common than those of mammals, and although fewer taxa are presently recognized, they may ultimately prove to be the most diverse group represented in the 'E' Quarry deposits. So far only the penguins have been studied in detail (Simpson 1971, 1975, 1979), and the fact that both identified taxa represent new genera suggests that other birds may be equally distinctive.

The birds are a potentially valuable source of palaeo-environmental information. For example, at least two species of parrots are represented, and parrots no longer occur in the south-western Cape, being confined to wooded tropical and sub-tropical regions further north. While this may indicate a warm, wooded environment at Langebaanweg during the early Pliocene, the representation of marine birds, particularly the Procellariiformes, apparently indicates temperate conditions in QSM and PPM times, which is in keeping with other evidence (see p. 68).

However, a detailed analysis of available material is required before the palaeoenvironmental implications of the avifauna can be assessed. Better identification of the taxa represented is also necessary. For example, there are several passerines that are characteristic of the south-western Cape fynbos region today (McLachlan & Liversidge 1978), and the identification of such forms in the 'E' Quarry avifauna would support the evidence which indicates that the fynbos was being established locally during the early Pliocene (see p. 43).

A curious feature of the avifauna is the under-representation of obvious scavengers such as vultures and crows. Scavengers (hyaenas) are well represented amongst the mammalian carnivores, and the inferred presence of abundant animal carcasses at the time that the deposits were laid down suggests that avian scavengers should also have been common.

The potential importance of the birds as indicators of depositional environments was briefly discussed by Rich (1980).

Mammals are the best represented group in the 'E' Quarry fauna, both in terms of the number of specimens and the number of species. Marine, freshwater, aerial and terrestrial species are recorded, the latter predominating. The

mammals are also the most intensively studied group, although descriptive accounts of about half the identified taxa have yet to be published. There are apparently no extant species represented, and the described forms include four new genera and sixteen new species.

A preliminary study of the small mammals (insectivores, bats, rodents and hares) by Pocock (1976) revealed nothing obviously inconsistent with a late Cenozoic fauna from this region. The most commonly represented of the small mammals are fossorial forms (Chrysochloridae, Bathyergidae), which are today still common in the vicinity of Langebaanweg, and elsewhere in the south-western Cape. The small mammals are a potentially valuable source of palaeoenvironmental information. For example, the only described rodent, a new genus and species (*Eurytomys pelomyoides*) which is common in the QSM, is a primitive otomyinine, a group which is characteristic of well-watered environments. The presence of *Dendromus* and *Graphiurus* may be further evidence for a wooded environment in the area at the time that the deposits were laid down.

One primate only has been recorded from deposits in 'E' Quarry, and it is known from fewer specimens than all other species. The under-representation of this important order is discussed later (see p. 87).

The carnivores are still the most diverse of the mammalian orders represented in 'E' Quarry. They are known from a large number of often complete and well-preserved specimens, a situation which is remarkable in view of the generally poor representation of this group at other African localities of late Miocene and Pliocene age. Since the last summary statement on them (Hendey 1976a: 234–240), further studies have been published on the bear (Hendey 1977, 1980), hyaenas (Hendey 1978c), mustelids (Hendey 1978d), and the seal (De Muizon & Hendey 1980). However, only the accounts of the bear and mustelids can be regarded as complete at this stage. Much material belonging to other families is undescribed, and at least some of the recorded taxa require reinterpretation.

For example, an incomplete study of the civet material has suggested that two species may be represented, one being related to the living African civet (*Civettictis civetta*), while the other may be related to the late Pliocene/early Pleistocene *Pseudocivetta* (Fig. 17). Similarly, the material referred to the canid (*Vulpes* sp.) may also represent two species, one being a generalized form possibly related to later African *Vulpes*, while the second may be related to the late Pliocene/early Pleistocene '*Canis*' *brevirostris*. The difficulty in identifying the 'E' Quarry civet and canid specimens is evidently due to the material representing early stages of lineages which were only clearly differentiated later. This applies in the cases of other 'E' Quarry mammals as well (see p. 82).

Although the identification of, and comments on, the 'E' Quarry proboscideans made by Coppens *et al.* (1978) are probably substantially correct, this group requires further study. None of the *Anancus* specimens, which apparently represent a new species, has been described, and the relationship

between the 'E' and Baard's Quarry species (Hendey 1978a) has yet to be substantiated. An appreciable number of unstudied teeth of the elephant (*Mammuthus subplanifrons*) are now available, and they may contribute towards resolving the problems surrounding this unsatisfactory taxon.

The 'E' Quarry perissodactyls are palaeoenvironmentally significant since both the rhinoceros and the *Hipparion* are hyposodont forms, indicating the presence of grasslands, whereas most of the other large herbivores are woodland browsers. Although the study of the perissodactyls is largely complete, the *Hipparion* specimens warrant further attention directed at their implications in respect of the succession of strata in the vicinity of Langebaanweg. For example, it is the *Hipparion* from the Anyskop terrestrial deposits which suggests that they are broadly contemporaneous with deposits in Baard's Quarry (see p. 38). In addition, it is the *Hipparion* from the GM which supports the suggestion that this horizon may predate the QSM and PPM by an appreciable period (see p. 23).

The artiodactyls, which are predominantly browsers, are a well-represented and diverse group, ranging in size from a very small peccary to the giant *Sivatherium*. With the exception of the pigs, hippopotamus, and palaeotragine, all have now been described, although additional material of most species is available. The palaeotragine is of particular interest since, although Africa is the home of the only living palaeotragine (*Okapia johnstoni*), the post-Miocene history of this group is poorly known, and the 'E' Quarry species is comparatively well represented by both cranial and postcranial material.

Other 'E' Quarry mammals which are unstudied are a pangolin, an aardvark, two species of porcupine, and several cetaceans.

Taphonomy

Taphonomy 'involves all aspects of the transference of organic remains from the biosphere to the lithosphere, and includes both the biological and physical factors and processes that are involved' (Olson 1962: 134). It is, therefore, a branch of palaeontology that is particularly relevant to palaeo-ecological studies. Some information of a taphonomic nature, such as the mode of accumulation of many of the 'E' Quarry fossils, has been given above, and the summary account which follows deals with other matters.

A taphonomic study of the 'E' Quarry fossils such as the now classic one on a late Tertiary vertebrate fauna from Nebraska by Voorhies (1969) has not been undertaken. Nevertheless, almost unavoidably observations of a taphonomic nature have been made in the course of fieldwork at Langebaanweg, and subsequently also in the laboratory. Some of these observations have already been recorded elsewhere (Hendey 1974a: 348-353; 1976a: 222-230; 1980: 53-67).

In any assessment of the taphonomy of individual fossil assemblages from 'E' Quarry, it is important that allowance be made for collecting biases, recent damage to bones and the post-depositional disassociation of body parts. Conse-

quently, the manner in which material was acquired needs to be known. specimens were recovered from the 'E' Quarry sediments in the following ways:

1. Surface collecting.
2. Controlled excavation.
3. Uncontrolled excavation.
4. Screening of small sediment samples in the field or the laboratory using mesh of 2 mm or less.
5. Screening of bulk sediment samples in the field using a double-bank of sieves with mesh of 10 and 5 mm.

In the case of surface collecting, material had mostly been exposed by the mining operations, in which case specimens were often out of context, damaged and disassociated from other skeletal elements of the individual involved. A large quantity of material was acquired in this way, with most specimens being of medium to large size. Alternatively, specimens were exposed by wind or water erosion, in which case their condition was often as in burial, and associations of specimens were sometimes preserved. Once again much material was collected in this way, and all except microscopic specimens were recovered.

Only a few controlled excavations were undertaken in 'E' Quarry, two in 1966 and one or two in the years 1969, 1970, 1975, and 1976. However, although most of the fossiliferous horizons and areas of the QSM and PPM were sampled, the size of the excavations was very variable, ranging from a few to hundreds of cubic metres of deposit. The condition of specimens for the most part reflects that in burial, and associations were recorded. Uncontrolled excavations differed in that they were always on a small scale, usually being centred on a significant fossil discovered on the surface (Fig. 13). Except for the recording methods, they could be considered as controlled excavation when carried out by qualified personnel, but otherwise they served only to build up sample sizes.

It was the latter factor, together with the need to recover small fossils, that was the motivation in the screening of sediment samples. The screening of small samples usually involved the use of hand-sieves washed in ponds on site, or in containers of water in the laboratory. Since the deposits were mostly unconsolidated fine- to medium-grade sands, little agitation of the sieves was required and damage to specimens was minimal. However, associations of body parts were usually lost.

The co-operation of the mining company made the screening of bulk sediment samples possible. This was done when mining or other factors threatened fossiliferous deposit, and involved the removal by mechanical means of samples ranging in size from a few tons to hundreds of tons, and the transportation of the sample by truck to an area where a stand with double-banked two-man sieves was set up. Piped water was used to wash the 'dumps' through the sieves. This process allowed the recovery of some very large samples of fossils, and was particularly useful in the recovery of rare taxa. However, the process which variously involved mechanical excavators, bull-



Fig. 13. The skull and vertebral column of a buffalo *Simatherium demissum*, (SAM-PQ-L23400) *in situ* in the QSM.

dozers, front-end loaders, and tip-trucks, was very destructive. In addition, there were instances where the removal process was not carefully controlled and fossiliferous sediments of the QSM and bed 3aN were mixed.

The provenance of material was one of the recurrent problems encountered in the fossil-collecting programme. Material of doubtful provenance includes much of that collected prior to 1969, but the problem continued even when the nature of the succession was well known and exact sites of discovery were recorded. Both beds 3aS and 3aN truncated the QSM, while bed 3aN truncated bed 3aS, and it was in such situations that doubts about provenance arose. Nevertheless, assemblages of known provenance do exist, and it is these that will ultimately be used in the detailed analyses of fossils from particular horizons. A problem which may be impossible to deal with is that of material reworked from pre-existing deposits. It affects mainly bed 3aS, which includes specimens derived from the QSM.

The depositional environments of the 'E' Quarry succession need not be discussed again, but some comments on the agencies responsible for concentrating fossils in certain areas are necessary.

The principal agency involved was water action. In the case of the GM fossils, concentration was by wave action, and in QSM III it was the combined effects of the river and tides which led to the accumulation of fossils. Elsewhere in the QSM and in beds 3aS and 3aN the river was largely responsible for concentrating fossils deposited in a subaqueous environment, although a subsidiary role for wave and tidal action cannot be ruled out.

One of the common field practices in taphonomic studies is the recording of the orientation of *in situ* fossils, since the resultant data may indicate whether or not the fossils were deposited by flowing water, and, if so, the current direction(s). In one of the earlier controlled excavations in 'E' Quarry (LBW/E/1969/1) some such recording was done, but the procedure was abandoned since it was found to be time-consuming and probably pointless. It seemed obvious at that time that the deposits in question (bed 3aS) were channel-laid and that the trend of the channel was north-east to south-west. All subsequent observations on the bed 3aS deposits confirmed this early impression. Much the same applied in the case of the bed 3aN deposits (see Hendey 1976a: 228–230; 1980: 57–63), although in this instance the nature and distribution of the fossils were much more obviously indicative of a fluvial environment.

Evidence for the subaerial accumulation of some QSM fossils has been discussed elsewhere (Hendey 1974a: 349–353; 1976a: 223–224). This includes the record of a vertebrate microfaunal concentration, apparently an owl pellet accumulation, which was burnt prior to incorporation in the deposits. Microfaunal concentrations of this kind were not common in 'E' Quarry. The most notable examples were two that occurred at the interface between the QSM and bed 3aS. These assemblages, designated 1/1968 and 12/1968, were discussed by Hendey (1970a: 81, 86–88), and remain something of a mystery. They are probably comprised largely of the residues of owl pellet accumulations which were transported a short distance and redeposited by minor drainage channels in QSM or bed 3aS times. This process would account for the admixture of larger fossils which obviously did not feature in the diet of owls. Two species of owls are recorded from the QSM.

Otherwise there is no evidence for animals having been 'bone collectors' during the period of deposition of the 'E' Quarry deposits. Elsewhere in the south-western Cape concentrations of fossils in porcupine lairs and hyaena dens have been recorded (Hendey 1974a; Klein 1975). Some of these are in rock shelters, of which none existed in the 'E' Quarry area, while others are found in what are presumed to be aardvark burrows. Such burrows would not be expected in the largely subaqueously deposited PPM, and it is unlikely that any existed on the floodplain of the river in QSM times. An aardvark is recorded from the QSM, but it is an extremely rare element in the fauna. The aardvark remains from beds 3aS and 3aN were probably washed into the area by the river.

Large numbers of fossils were found in certain exposures of the QSM, although not necessarily concentrated in restricted areas. For example, the remains of small mammals and birds were abundant in the QSM I collecting area named 'East Stream' (Hendey 1974a, fig. 3). The East Stream fossils probably represent a microenvironment (floodplain grassland or thicket) in which predation by small carnivores (mainly mongooses) occurred frequently. Larger mammals that died there include an elephant (*Mammuthus subplanifrons*) several pigs (*Nyanzachoerus* cf. *pattersoni*), a large cat (*Dinofelis dias-*

temata), and hyaenas (*Hyaena abronia*). Some redistribution of animal remains apparently took place when this area was inundated during floods (Hendey 1974a: 351–352; 1976a: 223–225).

An impression gained during field and laboratory work was that the body part representation of vertebrates varied according to the source of material. The only body part analyses undertaken to date are those of bird remains from the QSM I and QSM II assemblages (Rich 1980), to which may be added the detailed record of the number and condition of penguin bones from QSM I given below. Many more such analyses are required before meaningful taphonomic interpretations are obtained, but some general statements on body part representation are already possible.

Complete skeletons were not found, although partial skeletons were recovered from both the QSM and PPM. The most complete was that of the holotype of *Hyaena abronia* from QSM I, which comprises the skull and about eighty postcranial bones (Hendey 1974a: 103–115, 351–352). Otherwise elements of individual skeletons tended to be completely disassociated, or represented by only a few bones such as parts of a vertebral column or limb. Even in the latter instances it was exceptional to find bones still articulated. An example of a partial skeleton from the QSM in which some elements were in articulation is that of the buffalo illustrated in Figure 13. It is one of several medium to large mammals from the QSM which probably represent the remains of animals killed *in situ* and subsequently dismembered by the primary predator and by scavengers (Hendey 1974a: 351).

By contrast, the recently described partial skeleton of an *Agriotherium* (SAM-PQ-L45062) from bed 3aN, in which all remaining skeletal elements were disassociated (Hendey 1980: 62–63), was a more common type of occurrence. In this instance, the specimen was transported to its point of deposition by the river and it might well have been complete when deposited, but suffered subsequently from a variety of destructive post-depositional processes, including disarticulation after loss of soft tissue, fire, pressure of overlying deposits, and, more recently, the mining operation and collecting.

It is virtually certain that the skull of L45062 was intact at the time of deposition and that its subsequent fragmentation was due largely to the pressure of overlying deposits. Complete, or nearly complete, skulls are not common in the 'E' Quarry assemblage, and all the known specimens suffered some degree of crushing. Restoration of these specimens was, however, facilitated by the fact that fragments were easily recovered from their unconsolidated matrix and were usually undistorted. Missing parts were probably lost during the recovery process rather than earlier. One of the most complete skulls recovered is illustrated in Figure 17, while others have been illustrated elsewhere (e.g. Hendey 1974a, figs 19–20; Gentry 1980, figs 28–29; De Muizon & Hendy 1980, figs 1–3, 5). One instance is known where an exceptionally robust skull might have been intact in the deposits but was damaged by the mining operation. This is the skull of the *Plesiogulo*, SAM-PQ-L40042, described by Hendey (1978d: 330–336).

In general, the fossils from 'E' Quarry are well preserved, although damage caused by post-mortem processes is not uncommon. These processes include the mining operation and collecting methods which led to the recovery of specimens, and they are obviously of no taphonomic significance. Nevertheless, it is important that they be recognized and not be confused with that post-mortem damage which is relevant to taphonomic studies.

This damage is significant since it reveals some of the physical, chemical and biological processes which affected animal remains from the time of death until their discovery. From a palaeoecological point of view it is the factors operating at the time of death and shortly thereafter that are important, since they may reveal something of prevailing biological interactions and physical conditions. For example, the activities of predators and scavengers may be revealed by distinctive types of damage and thus provide evidence of trophic relationships, while the condition of specimens may also indicate the nature of depositional environments, which are a reflection of the prevailing physical environment.

The bed 3aN *Agriotherium* may again be cited as an example, since the recently discussed post-mortem damage to the specimens (Hendey 1980: 63–66) is typical of that encountered amongst the larger mammals from 'E' Quarry. Similar and additional types of damage were discussed elsewhere (Hendey 1974a: 349–353). Table 4 lists various types of post-mortem damage evident in specimens from 'E' Quarry. Only one of the more unusual types of damage is discussed below, since the example cited has not previously been recorded.

Hendey (1974a: 353) mentioned a series of bones from the QSM which had apparently been etched by the stomach acids of a hyaena. Such specimens are not common, but one striking example involves the penguins from 'E' Quarry. Two penguin species are recorded, namely, *Inguza predemersus* and *Dege hendeyi* (Simpson 1971, 1975, 1979), and a high proportion of the bones in the available assemblages have been etched, evidently by stomach acids (Fig. 14). By contrast, this type of damage is either rare or not recorded in bones of other birds from the same deposits.

The most likely explanation of this difference in condition is that the penguins were preyed upon by an animal that ingested their carcasses and later regurgitated the indigestible remnants, whereas other bird bones found in the deposits were not ingested by predators. It is only the stouter and more durable bones of the penguin skeleton which have been recorded (i.e. mainly limb bones). While other bones of the skeleton are less diagnostic, and therefore less likely to be recognized as belonging to penguins, their absence is probably due to their having been destroyed by the stomach acids which damaged most of the surviving bones. The most delicate of bones belonging to other birds are preserved together with those of penguins, which indicates that the effects of depositional processes can be eliminated as the cause of the condition and representation of penguin bones.

Modern penguins are preyed upon by sharks and other large predaceous fish, and seals (Simpson 1976), and these animals are all possible predators in

TABLE 4
Examples of post-mortem damage exhibited by fossils from 'E' Quarry, Langebaanweg.

TYPES OF DAMAGE	Cracked and exfoliated bones and teeth	Crushed bones	Abraded bones and teeth	Bones and teeth discoloured black* and/or grey, and often cracked and exfoliated	Etched bones
PROBABLE CAUSES AND ILLUSTRATIONS	Pre-depositional subaerial weathering; post-depositional subaqueous weathering (e.g. in lag deposits)	Post-depositional pressure of overlying deposits (especially affecting mammal skulls—e.g. Hendey 1980, fig. 2)	Wave action; river transport; sand-charged water flowing over specimen after deposition (fig. 3)	Fire (Hendey 1980; fig. 30)	Stomach acids of carnivores (Fig. 14) (Simpson 1975; figs 4-5; 1979, fig. 1)
TYPES OF DAMAGE	Spirally fractured bones	Punctate marks on bones	Irregular grooves, randomly orientated on bones, sometimes with irregular loss of adjacent bone	More or less parallel grooves on bones	Regular grooves, randomly orientated on bovid horn-cores
PROBABLE CAUSES AND ILLUSTRATIONS	Biting by carnivores (Hendey 1974a, fig. 77A)	Biting by carnivores (Hendey 1974a, fig. 77B)	Biting and gnawing by carnivores (Hendey 1974a, figs 77C, D; 1980, fig. 28)	Gnawing by rodents (Hendey 1980, fig. 29)	Keratophagous insect larvae (Fig. 12)

*Fossils from the 'peat beds' of the QSM and PPM, bed 3aN are also black, but they are usually readily distinguishable from burnt specimens.



Fig. 14. Undamaged (above) and acid-etched (below) penguin tibiotarsi, femora and carpalometacarpi from the QSM (East Stream sample).

the case of the 'E' Quarry penguins. In addition, penguins are preyed upon by terrestrial animals, and 'E' Quarry is unique amongst recorded Tertiary penguin localities in that the penguin bones come from non-marine deposits (Simpson 1976) occurring in association with a wide variety of terrestrial vertebrates, including predaceous forms. Consequently, it could also be significant that 'E' Quarry is apparently the only known locality from which penguin bones etched by stomach acids have been recorded. In fact, the 'E' Quarry penguins are likely to have been preyed upon by several aquatic and terrestrial predators, although only one is likely to have caused the acid-etched bones. This was probably an animal that bolted its food, and subsequently regurgitated indigestible residues. This behaviour applies in the case of sharks (P. A. Hulley, pers. comm.), and of the predators recorded in association with the 'E' Quarry penguins, sharks are here favoured for the role.

Further clues concerning predation on the 'E' Quarry penguins may emerge from more detailed examinations of the available material and comparisons with stomach contents of modern penguin predators. Even the most superficial examination of the 'E' Quarry penguin assemblages reveals features that may be of taphonomic significance. For example, etching is more pronounced on leg bones than those of the flipper (Table 5). In addition, certain

TABLE 5

Limb bones of adult penguins (QSM I, East Stream sample) from 'E' Quarry, Langebaanweg.

	<i>Inguza predemersus</i>			<i>Dege hendeyi</i>		
	Specimens with little or no etching	Specimens with pronounced etching	Specimens % etched	Specimens with little or no etching	Specimens with pronounced etching	Specimens % etched
Humerus . . .	3	6	67	—	—	—
Ulna . . .	6	10	63	—	1	100
Radius . . .	6	8	57	1	—	0
Carpometacarpus	4	3	43	—	—	—
Total flipper .	19	27	59	1	1	50
Femur . . .	3	9	75	3	7	70
Tibiotarsus . .	2	19	90	1	4	80
Tarsometatarsus .	1	15	94	2	4	67
Total leg . . .	6	43	88	6	15	71

TABLE 6

Etching on penguin leg bones (QSM I—East Stream sample) from 'E' Quarry, Langebaanweg.

	<i>Inguza predemersus</i>			<i>Dege hendeyi</i>		
	Little or no etching	Pronounced etching	% etched	Little or no etching	Pronounced etching	% etched
Femur, proximal end .	4	5	56	7	1	14
Femur, distal end . .	2	7	78	2	6	75
Tibiotarsus, proximal end .	1	9	90	1	1	50
Tibiotarsus, distal end . .	4	8	67	1	3	75
Tarsometatarsus, proximal end .	—	13	100	—	5	100
Tarsometatarsus, distal end . .	5	10	67	1	5	83

parts of individual bones are more affected than others. For example, the proximal ends of femora are less often etched than distal ends, while all the proximal ends of the tarsometatarsi are etched, and, at least in the case of *Inguza predemersus*, the proximal ends of the tibiotarsi are more affected than distal ends (Table 6). Furthermore, although there is a general similarity in the condition of the bones of the two penguin species, there are very marked differences in the representation of individual bones. This may simply be due to the smaller *Dege hendeyi* sample size, but it is striking that whereas there are nearly as many femora of *D. hendeyi* (ten) as there are of *I. predemersus* (twelve), other limb bones of the former are appreciably less common. This applies particularly in the case of flipper bones (Table 7).

TABLE 7
Flipper and leg bones of penguins (QSM I—East Stream sample)
from 'E' Quarry, Langebaanweg.

	<i>Inguza predemersus</i>	<i>Dege hendeyi</i>	<i>Dege: Inguza</i>
Total flipper . . .	46	2	1:23
Total leg	95	21	c. 1:5
Flipper: leg	c. 1:2	c. 1:10	

The above observations are not interpreted here, but they presumably reflect events which followed shortly after the deaths of the birds concerned, and thus indicate a potential value in analyses of this kind.

Certain of the 'E' Quarry fossils also reveal something about the condition of animals during their lifetimes, and although this does not necessarily fall within the scope of taphonomy, it is convenient to mention it here. The majority of specimens show no signs of abnormality, but pathological conditions amongst carnivore specimens have already been recorded (Hendey 1974a: 184–185; 1978d: 336; 1980: 53), while abnormalities observed amongst herbivores will be mentioned later (see p. 76). The latter are ascribed to dietary factors, but most of the other recorded conditions are evidently due to old age or injury. Apart from their intrinsic interest in the field of palaeopathology, dental and osteological abnormalities are significant since they may provide evidence of prevailing environmental conditions, the age structure of populations, cause of death, and behaviour patterns. Consequently, a detailed study of relevant specimens is clearly desirable.

PALAEOENVIRONMENT

The nature of environments in the south-western Cape and adjacent regions during the Palaeozoic, Mesozoic, and early Cenozoic are known only in a very general way, but the record for the late Cenozoic is better (Deacon 1979). However, even for this period the record is only intermittently detailed,

and for the late Tertiary it is the deposits in the vicinity of Langebaanweg that provide the most substantial body of information.

The environment at Langebaanweg at the time that the Varswater Formation and other late Tertiary deposits were laid down was clearly very different from that of the present. An account of the physical setting of the area and of the geological history of these deposits was given earlier, and the present section will deal with the climate and the environmental implications of the Varswater Formation flora and fauna. It is important to note that information presented below contributed to the revised interpretation of the geological history of the Langebaanweg area. In other words, although these two aspects of the present study are interrelated, the interpretation of the geological history stemmed in part from the palaeoenvironmental study rather than the reverse, which is implied by their order of appearance in this report.

The late Miocene and early Pliocene (i.e. between about 10 and 4 Ma) was a period of great change over much of the earth's surface. It was the time when the generally moderate climatic conditions which characterized most of the Tertiary were coming to an end, and when the most recent of the world's 'ice ages' was beginning. This 'ice age' has been a period of marked oscillations in world climates, and these have had a profound effect on the biology of the earth.

The Miocene-Pliocene boundary is defined on the basis of the marine sedimentary succession in the Mediterranean Basin, and it is now generally taken to date back about 5 Ma, with marine microfossils and palaeomagnetic data having facilitated widespread correlations (e.g. Berggren & Van Couvering 1974). Apart from changes in marine microfaunas, the terminal Miocene was characterized by a world-wide marine regression, a phenomenon that was caused by increased glaciation in Antarctica (see below), and which had significant effects in coastal and continental shelf regions of the world.

In the Mediterranean this regression contributed to the so-called 'Messinian [or Mediterranean] salinity crisis', which 'was an interval of highly restricted circulation reflected in extensive deposition of stagnant water and evaporative sediments' (Van Couvering *et al.* 1976: 263). This event, which lasted approximately 1,5 m.y., was concluded by 'a return to former water depths coincidentally with the beginning of the Pliocene . . . which is calibrated to $t = 5$ Ma' (Van Couvering *et al.* 1976: 263). Hsü *et al.* (1977: 402) have stated that the Messinian salinity crisis is 'such a geologically recent catastrophic event [that it] had a great impact on the modern world, . . . on regional and global climates and on the evolution and distribution of plants and animals'.

An example of the biological impact of this event was that it allowed the late Miocene faunal interchange between Africa and Eurasia which will be mentioned later (see p. 84), and hence the presence in the 'E' Quarry fauna of certain 'Eurasian' taxa. However, the principal significance of the Messinian event here is that it is well documented and thus illustrates the nature and timing of certain of the *global* phenomena that occurred during the late

Miocene and early Pliocene. For example, the Messinian event was simply one result of the increased late Miocene Antarctic glaciation and the consequent global marine regression, which are events of far greater significance in the present instance. Langebaanweg is situated in southern mid-latitudes, 7 500 km south of the Mediterranean, whereas it is only 4 000 km from Antarctica, and separated from it by an ocean that influences the climates of both regions. In addition, its near-coastal location makes it subject to the effects of sea-level changes.

In a recent review of late Cenozoic palaeoenvironments on the west coast of southern Africa, Tankard & Rogers (1978) related the aridity of this region to the history of the Southern Ocean and the Antarctic ice-cap. Although there are many conflicting statements on the timing of Antarctic ice-cap origin and growth (see Mercer 1978), there is evidence that maximum growth was achieved late in the Miocene (see McLachlan & McMillan 1979, fig. 2). Once the Antarctic ice-cap had formed it 'remained a semi-permanent feature exhibiting some changes of volume', 'the most important [being] during the latest Miocene ($t = 5$ MY ago) when ice volumes increased beyond those of the present day' (Kennett 1978: 41). This was followed by 'a regressive ice phase with extensive melting and iceberg calving' (Hayes *et al.* 1973: 24). The glacial maximum led to the terminal Miocene global marine regression (cycles TM3.2, TM3.3 of Vail & Hardenbol 1979), while the subsequent regressive ice phase caused the early Pliocene global transgression (cycle TP1).

The fact that these events are correlated not only with the Messinian salinity crisis and its conclusion, but also with coastal strata elsewhere (e.g. New Zealand—see Loutit & Kennett 1979), suggested that correlation with Miocene–Pliocene strata in South Africa is also feasible.

Relevant here is evidence that local sea temperatures declined during the period of deposition of the Varswater Formation.

Present sea temperatures on the Cape west coast are low, and the area falls within the Cold Temperate Province of the southern African coast (Brown & Jarman 1978). However, the coast near Langebaanweg is close to the southern boundary of this province and the western limit of the 'overlap region' between the Cold and Warm Temperate Provinces (Brown & Jarman 1978: 1246). This 'overlap region' includes areas where the proportion of cold west coast species is high, and others, such as False Bay, where 'south coast species are much in evidence' (Brown & Jarman 1978: 1261). The northern shore of False Bay is at present only about 130 km south of Langebaanweg, and during the past when sea-levels were substantially higher, this bay was linked across the Cape Flats with Table Bay, 20 km further north. Furthermore, Langebaanweg is today only 13 km inland from the 'almost landlocked body of water comprising Langebaan Lagoon and Saldanha Bay', with its 'biota of great richness, diversity and productivity' that includes species that 'are characteristic of other provinces, notably the south coast warm-temperate region' (Brown & Jarman 1978: 1267).

Langebaanweg is thus situated in an area where the local marine fauna is potentially subject to marked differences in composition depending upon

prevailing climatic and environmental factors. Even today elements of two contrasting faunas (warm and cold temperate) are represented near by (Langebaan Lagoon, Saldanha Bay), or not far away (False Bay), while the local occurrence of thermally anomalous molluscs during the late Pleistocene has been documented by Tankard (1975*d*).

Molluscs of the GM are mostly of taxa found along the adjacent coast today, but some 'suggest water temperatures considerably warmer (about 3–5 °C) than today. These warm water molluscs include *Cellana capensis*, *Turbo sarmaticus*, *Barbatia obliquata*, *Ostrea atherstoni*, and *Striostrea margaritacea*' (Tankard 1974*a*: 281). The oysters *Ostrea* and *Striostrea* are not known from 'E' Quarry exposures of the GM, but are from equivalent deposits on the near-by farm of Sandheuwel (Tankard 1974*a*). *Cellana capensis* is today found north of Port Alfred on the east coast (i.e. the Subtropical Province), while the other four species occur eastwards from False Bay (i.e. the Warm Temperate and Subtropical Provinces) (Kensley 1973; Day 1974; Brown & Jarman 1978).

In addition, although the sharks of the GM have yet to be studied in detail (Hendey 1976*a*: 233), three of the species that have been recorded are today characteristic of warmer oceanic regions. They are *Carcharhinus melanopterus*, *C. limbatus*, and *Squatina africana* (Bass *et al.* 1973, 1975).

Indications are, therefore, that the GM was laid down during a warm phase (i.e. warm temperate to subtropical), probably the period late in the Miocene that preceded the onset of colder conditions towards the end of this epoch.

Molluscs of the QSM are also mainly of taxa found along the adjacent coast today, although one is a warmer water species. This is *Pyrene albuginosa*, which presently ranges from False Bay to Natal. On the other hand, the QSM assemblage, unlike that of the GM, also includes two essentially cold-water species, namely, *Chiton nigrovirescens* and *Tricolia capensis*, which are largely confined to the Cold Temperate Province of the west coast. In this instance, *T. capensis* is particularly significant, since it is the most commonly occurring of the QSM marine species (Kensley 1977).

It is, therefore, likely that local sea temperatures at the time of deposition of the QSM were somewhat lower than those prevailing earlier when the GM was laid down, and might have been little different from those of the present (i.e. cold temperate). Consequently, the QSM is likely to date from the period when the effects of Antarctic glaciation were being manifested in southern mid-latitudes (i.e. terminal Miocene or later).

A similar, and probably contemporaneous, change from warm to cold water is recorded on the west coast of South America. Mercer (1978: 80), quoting W. J. Zinsmeister, noted that the 'presence of distinctly warm-water genera of molluscs indicates that during Middle and Late Miocene time the coastal waters of southern Chile were warm subtropical', and that these 'warm-water faunas were replaced by distinctly cool temperate faunas in latest Miocene or earliest Pliocene time'.

Although no identifiable molluscs are recorded from deposits overlying the QSM (i.e. the PPM), remains of another marine species, the seal (*Homiphoca capensis*), suggest that either there was a further temperature drop in the period between deposition of beds 3aS and 3aN, or that temperatures remained consistently cold during this period. The evidence for this concerns the greater development of the maxillo-turbinals in the bed 3aN population of *H. capensis* (De Muizon & Hendey 1980: 123). This adaptation to low sea and ambient air temperatures may either reflect a lowering of such temperatures during the period in question, or a delayed reaction to the prevailing cold conditions. In the case of the latter alternative, the implication is that the cold adaptation in *H. capensis* lagged behind the onset of the cold. This may be a more reasonable supposition in the case of a large mammal than the one that would have the adaptation immediately coincident with the temperature change.

It is worth noting in this connection that *H. capensis* was almost certainly resident in the Langebaanweg area, and consequently that the cold adaptation reflects local conditions. *H. capensis* was definitely not represented by occasional vagrant individuals as is the case today with certain Antarctic and sub-Antarctic seals recorded on the Cape coast (e.g. *Mirounga leonina*, *Lobodon carcinophagus* and *Hydrurga leptonyx*). The presence of the remains of very young, probably neonate, individuals in the 'E' Quarry assemblage indicates that breeding took place in the immediate vicinity. Otherwise the individuals represented range from young to very old, and at least in beds 3aS and 3aN they are present in large numbers, indicating large local populations at the time of deposition.

In addition, it is unlikely that *H. capensis* was seasonally migratory. Its dental and postcranial characteristics suggest it was a coastal species, unlike its closest living relatives, the pelagic crabeater and leopard seals (*Lobodon carcinophagus* and *Hydrurga leptonyx*) (De Muizon & Hendey 1980). These two species are migratory, moving southwards during summer when the pack-ice begins to break up (King 1964). Southward migration during summer was probably characteristic of all the southern middle and high latitude migratory seals that are now extinct, and since beds 3aS and 3aN were probably laid down during summer (see p. 73), *H. capensis* evidently did not follow this practice.

Other evidence of prevailing temperatures may yet be obtained from a study of the QSM and PPM avifaunas. There are indications that the avifaunas also reflect cold conditions (see p. 54), but this has yet to be substantiated.

Available evidence therefore indicates a lowering of sea temperatures during the period between deposition of the GM and QSM, and either a further drop between deposition of beds 3aS and 3aN, or consistently low temperatures at that time. Although there is as yet no positive evidence of what occurred between deposition of the QSM and bed 3aS, it is unlikely that there was a deviation from the generally cold conditions otherwise indicated, since the QSM, bed 3aS and bed 3aN represent deposition during a single geological episode (i.e. a marine transgression). Sea temperatures were low at this time

apparently because it followed immediately after the terminal Miocene glacial maximum in Antarctica. Temperatures might have risen again later in the early Pliocene transgression (see p. 16).

Thus, while deposition of the GM probably took place before the onset of the terminal Miocene glacial maximum, the QSM and PPM are likely to post-date this event. This conclusion, taken in conjunction with others discussed in this report, contributed to the correlation of the 'E' Quarry deposits with the late Miocene–early Pliocene events in Antarctica, the Mediterranean Basin and elsewhere. This correlation is summarized in Table 8, which formed the basis of the correlation of the entire late Tertiary succession in the Langebaanweg area with the global sea-level changes recorded by Vail & Hardenbol (1979) (Fig.3, Table 2).

To sum up, the GM is here interpreted as representing an event dating back to a warm phase during the late Miocene, while the post-GM regression is correlated with the world-wide lowering of sea-level which coincided with the glacial maximum in Antarctica during the terminal Miocene (i.e. between 5,5 and 5 Ma—see Van Couvering *et al.* 1976). Amongst other significant events, this regression has been correlated with the climax of the Messinian salinity crisis, and the formation of phosphate nodule beds in Australia and elsewhere in the world (Carter 1978). The transgression during which the QSM and PPM were laid down is in turn correlated with the regressive ice phase in Antarctica during the early Pliocene, between 4,5 and 5 Ma (Van Couvering *et al.* 1976). This transgression, which is recorded in countries as far apart as Spain and New Zealand (Loutit & Kennett 1979), brought the Messinian salinity crisis to an end. This interpretation of events indicates that the main exposures of the Varswater Formation in 'E' Quarry (i.e. the QSM and PPM) are of the same age as the early Pliocene deposits in the Mediterranean Basin (including those at Montpellier in France), and at least part of the Opoitian Stage in New Zealand. Correlation with other early Pliocene coastal deposits is clearly possible.

One possible inconsistency with this interpretation concerns the suggestion that sea temperatures might have declined during the period of deposition of the QSM and PPM. Since the early Pliocene transgression post-dates the late Miocene glacial maximum in Antarctica, it would be expected that sea temperatures in southern mid-latitudes would be rising at this time. However, according to Hayes *et al.* (1973: 24) 'the waters around [Antarctica] would not necessarily exhibit warming at that time but simply a slowdown in the rate of cooling'. At issue here is the nature and timing of events in Antarctica during the late Tertiary, and, according to at least some interpretations, Southern Ocean surface temperatures did decline during the early Pliocene (Mercer 1978: 84–86, fig.4). This is consistent with palynological evidence from the south-western Cape that suggested to Coetzee (1978: fig.2) that the local climate changed from 'Cool Wet' during the late Miocene to 'Colder Drier' during the Pliocene.

There is abundant evidence from various parts of the world that the Miocene and Pliocene were epochs when terrestrial environments were under-

TABLE 8
The Varswater Formation, 'E' Quarry, Langebaanweg.

STRATIGRAPHIC UNITS	PRINCIPAL DEPOSITIONAL ENVIRONMENTS	SEA-LEVEL	SEA TEMPERATURES	CLIMATE	POLLEN ZONES** AND VEGETATION	AGE
VARSWATER FORMATION	Marine littoral	Transgression (cycle TP1*)	Cold temperate	Temperate; colder and drier than before**	Lvii (in part)** Temperate woodlands and grasslands; first strong development of the fynbos**	<div>Time interval</div> <div>Time interval</div> <div>Early Pliocene (c. 5.0 Ma)</div>
	Fluviatile					
	Fluviatile					
	Estuarine and terrestrial					
PELLETAL PHOSPHORITE MEMBER	PPM, 3aN, 3aS QUARTZOSE SAND MEMBER (QSM)	No deposits	Probably cold temperate	Temperate	Temperate woodlands and grasslands	Terminal Miocene (6, 6-5, 2 Ma)
(PPM undiffer- entiated)		Regression (cycles TM3.2, 3.3*)	Warm temperate to subtropical	Warm temperate to subtropical (becoming cooler)	Lvi (in part)** Subtropical monsoon forest and grassland	Late Miocene (9, 8-6, 6 Ma)
PPM, 3aN, 3aS		Stillstand during regression (cycle TM3.1*)	Warm temperate to subtropical			

* Vail & Hardenbol (1979)

** Coetzee (1978)

going significant change. For example, Webb (1977: 355) has recorded that 'early in the Cenozoic Era North America was covered almost entirely by forest', and that 'during the mid-Cenozoic . . . an increasing proportion of the land opened up, forests giving way to woodland savanna, thorn forest, and thorn scrub', while 'by the late Cenozoic forested areas had decreased still further and much of the savanna was being replaced by grassland steppe and even desert'. Webb (1977: 371) also states that 'the last step in dismantling the once continuous forests of North America came in the Pliocene, about five million years ago'. He goes on to note that 'a remarkably similar series of changes affected the fauna of temperate South America during the same 40-million-year interval' (Webb 1977: 355).

Kemp (1978) has recorded the environmental changes undergone in the south-east Indian Ocean region during this period and, amongst other observations, she noted that the 'latest Miocene was marked by an intense and sudden chilling [which] must have caused marked precipitation decrease in much of Australia' (Kemp 1978: 170). These and subsequent climatic events had a pronounced affect on the vegetation of the continent. For example, Axelrod & Raven (1978: 112) recorded that 'evidence in south-eastern Australia . . . [indicates] that the transition from a humid temperate rainforest to the present dominant *Eucalyptus-Acacia* vegetation occurred at ~ 4.5 m.y. (Gill 1975)'.

There were comparable changes in Europe at this time. Delson (1975: 46) has suggested that the deterioration in the European environment late in the Miocene was determined largely by 'relative decrease in moisture', there being 'a gradient from well-watered deciduous (or even evergreen) woodland in the north, through parkland, scrub and into steppelike vegetation . . . with gallery forests along watercourses'. The situation in southern Europe is relevant in the present instance, since those areas bordering the Mediterranean now have a climate similar to that of the south-western Cape, and changes undergone in the two regions during the late Tertiary are likely to have been comparable.

The faunas of Langebaanweg and Montpellier in southern France are broadly contemporaneous and similar in composition (see p. 89), and these localities are similarly situated in near-coastal environments which today have a Mediterranean type of climate. Consequently, it is possible that conclusions reached concerning the palaeoenvironment of Montpellier early in the Pliocene are relevant in the case of Langebaanweg.

Delson (1975: 47), quoting Lobreau-Callen & Suc (1972), states that pollens from Montpellier indicate a 'monsoon/dry season climate', 'closely analogous to that of . . . North Vietnam'. Schulze & McGee (1978, table 1), following Köppen & Geiger (1936), have monsoon climate characterized by 'mean temperatures above 18 °C for all months', with 'forest-vegetation despite [a] dry season'.

There is evidence to suggest that these conditions might have prevailed in the Langebaanweg area during the period of deposition of the middle to late Miocene elements in the succession (i.e. the GM and the upper levels of the

pre-GM deposits), but that by the early Pliocene (i.e. QSM, PPM) they were changing, with the present climate and vegetation patterns being in the process of development.

The predominance of browsers amongst the QSM and PPM herbivores indicates that forests or woodlands existed in the area during the early Pliocene, probably having been present locally for an appreciable period. This is confirmed by palynological evidence from the upper levels of the pre-GM deposits, which also indicates that the forests of the time included tropical elements such as palms (J.A. Coetzee, pers. comm.). The local vegetation during at least a part of the middle to late Miocene might therefore have been of a monsoon-forest type. The presence of grazers in the QSM and PPM faunas indicates that by the early Pliocene grasslands had developed locally, while there is palynological evidence for fynbos vegetation types making an appearance (see p. 43).

At the time of deposition of the QSM and PPM, rainfall was strongly seasonal, with the wet season probably being summer. However, the rainfall regime was then apparently changing, and the summer-wet/winter-dry pattern was probably more characteristic of the late Miocene than the early Pliocene. This possibility, together with the likely vegetation, suggests the monsoonal combination of forest/dry season quoted above.

It has yet to be certainly established when the summer-dry/winter-wet rainfall pattern was first established in the south-western Cape, but there can be little doubt that the QSM and PPM date from a period when the transition was taking place; or was about to take place. According to Taylor (1978: 75) 'dry summers are of recent origin in southern Africa and probably only appeared at the beginning of the Pleistocene'. Axelrod & Raven (1978: 112) are more cautious in stating the 'there is no evidence that the summer-dry (mediterranean) climates in southern Africa existed before the formation of a major ice sheet on Antarctica (~ 5 m.y.)'. Although the fynbos vegetation is today centred on the south-western Cape winter-rainfall region, it evidently had its origins under summer-rainfall conditions (Levyns 1964; Axelrod & Raven 1978; Taylor 1978). Consequently, the fact that fynbos was being established in QSM times does not necessarily mean that the summer-dry/winter-wet pattern already existed then.

The situation in respect of prevailing temperatures during the Miocene and early Pliocene is less complex. It was suggested earlier that temperate conditions prevailed in QSM and PPM times, and conditions then may have been little different from those of today. The present mean annual temperature in the south-western Cape is about 17 °C, with a mean annual range of about 8 °C near the coast (Fuggle & Ashton 1979). The region is thus cooler than those with monsoon climates, but the temperature difference is not great. During warmer phases such as that during the Miocene when the GM and upper levels of the pre-GM deposits were laid down, temperatures characteristic of monsoon climates might well have prevailed.

Langebaanweg during the Miocene, like Montpellier during the early Pliocene, might therefore have had a monsoon climate and vegetation. The essential difference between these two localities was in the timing of a drop in temperature and its consequent affect on rainfall and vegetation. The glaciation of the Arctic lagged behind the glaciation of Antarctica, with the expansion of the Arctic ice-cap and sea-level ice dated to 3 Ma (Berggren & Van Couvering 1974). Thus, while conditions at Montpellier during the early Pliocene were still 'tropical', at Langebaanweg they had already moderated to 'temperate'.

In his account of the palaeoenvironments of the south-western Cape and adjacent regions, Deacon (1979, table 1) recorded that the Miocene was characterized by an 'alternation between dominance by tropical palm and temperate vegetation', while during the Pliocene 'ancestral fynbos communities' were established. The evidence for these changes comes from fossil pollens studied by Coetzee (1978), who found that there was a warm phase in the region during the late Miocene when the vegetation was palm-dominated. Coetzee dated this phase to 8 Ma, but since it immediately preceded the terminal Miocene temperate phase associated with the Antarctic glacial maximum, it could have lasted to about 6 Ma. Palms and a casuarina apparently persisted through the terminal Miocene cool phase (Coetzee's Pollen Zone Lvi), into the Pliocene (Pollen Zone Lvii), when species typical of the fynbos make their first strong appearance. Consequently, it is possible that even though temperatures were no longer favourable, vestiges of a pre-existing monsoonal vegetation were still in evidence at Langebaanweg when the QSM and PPM were being deposited.

Axelrod & Raven (1978: fig. 6C), following Greenway (1970), indicate that during the latter half of the Miocene (i.e. *c.* 15–7 Ma) the south-western Cape was an area of 'subtropical forest' bounded a little to the north of Langebaanweg by 'sclerophyll vegetation'. During the period of environmental transition that followed, the forest was replaced by the sclerophyll vegetation. The displacement of the forests was evidently a gradual process which was still under way at the time that the QSM and PPM were being laid down.

It seems then that the main fossiliferous deposits of 'E' Quarry date from a period of transition, when climate, vegetation and fauna were in the process of change. These sometimes astonishingly rich fossiliferous deposits represent a period when a previously hospitable environment was undergoing a marked change for the worse. It was colder and drier, perhaps with rainfall tending towards a winter rather than summer peak, but in any case with a pronounced dry season; the vegetation was changing from forests or woodlands to more open types (fynbos and grassland), while there was a corresponding change amongst the terrestrial vertebrates, with open-country forms making a strong appearance.

The fynbos of the south-western Cape, in contrast to some other vegetation regions in Africa, is a less favourable habitat for larger mammals, and although the situation was to vary in response to changing environmental conditions during the Pleistocene (Hendey 1974*a*; Klein 1980), the environmen-

tal deterioration early in the Pliocene brought to an end the period when mammals perhaps enjoyed their greatest success in this region. The Varswater Formation provides the final and, indeed, only local evidence of this period.

The inferred habitat preferences of many of the 'E' Quarry taxa were given earlier (see pp. 45–53). The habitats of invertebrates tend to be very specific, and the 'E' Quarry species were invaluable in determining the depositional environments of the horizons in which they occur. As a general rule, vertebrates are less useful in this respect, although they are usually indicative of the major habitat types, namely, marine, fresh water and terrestrial. For example, representatives of the marine environment include sharks, certain birds, the seal, and cetaceans; freshwater taxa include the otter and the hippopotamus. The majority of the vertebrates are, however, terrestrial forms, and it is this group that will be dealt with here, since some provide an additional insight into the nature of the environment at the time that the Varswater Formation was laid down.

Amongst the herbivorous mammals both woodland species (browsers) and grassland species (grazers) occur. While the former predominate in terms of the number of species, grazers were more commonly represented at certain levels in the succession, or areas within the mine, evidently because of the taphonomic factors in operation. For example the alcelaphines (*Damalacra neanica* and *D. acalla*), which were undoubtedly grazers although relatively primitive representatives of their group, were the most commonly occurring of the larger mammals in the bed 3aS channel deposits of the PPM.

Before analysing the significance of faunal representation at any given level or area, it would be desirable if minimum numbers of individuals were determined. This has yet to be done because in many instances assemblages are very large and the sorting of body parts and identification of taxa represented is incomplete. Nevertheless, some patterns of representation are already obvious.

It was stated elsewhere (Hendey 1980: 56) that the remains of certain woodland species were incorporated in the Varswater Formation with increasing frequency as deposition progressed. The example cited was that of the giraffids, *Sivatherium*, *Palaeotragus*, and *Giraffa*. Conversely, the grazing rhinoceros *Ceratotherium* is represented in decreasing numbers.

This was interpreted as indicating that either woodlands were an increasingly widespread habitat in the vicinity, or that taphonomic factors were such that the remains of large woodland species were incorporated in the deposits in increasing numbers, while those of a large grazer correspondingly decreased. The former alternative is less likely in view of the representation of other grazers. These include the alcelaphines, *Damalacra neanica* and *D. acalla*, which are common in the higher levels (beds 3aS and 3aN), but very rare lower down (QSM). If grasslands were, indeed, giving way to woodlands, then the alcelaphines would also have been represented in diminishing numbers.

It may, in fact, have been the reverse situation that led to the observed representation of woodland–grassland species, that is, a diminution of woodlands in the area. The deteriorating local environment probably caused wood-

lands to be increasingly confined to the immediate vicinity of the river, thus restricting the habitat available to browsing species. Such animals would then have been increasingly hard-pressed in exploiting the diminishing food resources, with an increase in mortality caused by starvation being likely. In addition, it is possible that as the rainfall pattern was changing from a summer to winter maximum, it became more irregular and perhaps even diminished. Droughts might, therefore, have been an added hardship confronting the fauna.

There is evidence that at least some of the 'E' Quarry browsers were ill-adapted to prevailing conditions by bed 3aN times. For example, teeth of *Sivatherium* from this level sometimes exhibit hypoplasia of the enamel (fig.15)



Fig. 15. A–C. Incisors of *Sivatherium hendeyi* from the PPM 3aN (unnumbered Dump 10 specimens), with hypoplasia of the enamel. D. A healthy specimen.

This condition results from disturbances in the formation of the enamel matrix during development of the teeth, and is a positive indication of ill-health in the immature individual (Scott & Symons 1974). The aetiology in the case of the bed 3aN *Sivatherium* is not known, but a nutritional inadequacy is most likely. Such inadequacies could be caused by reduced food resources.

A second dental abnormality observed amongst bed 3aN browsers, is irregular and excessive wear of teeth. Although this was observed in several of the bovid species, it is most common in the teeth of the reduncines and/or tragelaphines. There are problems in distinguishing the teeth of these animals (see below), but it is virtually certain that the abnormal bed 3aN specimens belong to the reduncines (mostly *Kobus subdolos*, but some *Kobus* sp. B), the

species most commonly represented by easily distinguishable horn-cores. Abnormal wear on the teeth (Fig. 16) is reminiscent of that which is often found in zoo animals that have been provided with inappropriate food. For example, abrasive food such as hay, which is suitable only for hypsodont grazers, causes excessive and irregular wear on the teeth of browsers. Living reduncines are grazers, but the 'E' Quarry species have teeth resembling those of the browsing tragelaphines (Gentry 1980: 255–256). The implication is that the bed 3aN reduncines were browsers that were including in their diet an abrasive food (probably grasses) to which they were ill-adapted.

Indications are, therefore, that by bed 3aN times at least some, and perhaps all, the browsing herbivores in the fauna were under stress, with mortality probably being higher than usual. Thus, it could have been the diminution rather than an increase in woodland habitats that led to the increased number of browsers being incorporated into the accumulating 'E' Quarry deposits.

It has previously been postulated that rainfall at that time was strongly seasonal and that the fossiliferous channel deposits of beds 3aS and 3aN represent flood-season accumulations (e.g. Henzey 1980: 60–62). Conversely, the subaerially accumulated fossils of the QSM accumulated during the dry season (Henzey 1976a: 223–225). These conclusions are based on the nature of the deposits and the incorporated fossils.

For example, burnt bone is a not uncommon element of the QSM and PPM assemblages, indicating that vegetation and/or peat fires were a feature of the area at the time of their deposition (Henzey 1980: 66–67). Since hominid activity can be excluded as a possible cause of fires, as can volcanic activity and



Fig. 16. Reduncinae upper and lower molars from the PPM 3aN (unnumbered Dump 10 specimens), showing abnormal and excessive wear.

rock falls, it is most likely that fires were started by lightning. Such fires could be expected only if a pronounced, and perhaps prolonged, dry season had left the vegetation and peat deposits desiccated and inflammable. These fires must have placed the fauna under additional stress. Firstly, animals trapped in the fires would be injured or killed. This would apply especially in the case of slow-moving forms, such as tortoises, and this could account for the large numbers of tortoises found in the QSM, with its component of fossils accumulated subaerially during the dry season (see above). Secondly, fires would have further reduced the food supply available to herbivores, aggravating a starvation problem caused by a deteriorating environment, and the drought which preceded the first thunderstorms of the rainy season.

Lightning as the cause of fires is itself of palaeoenvironmental interest. Under existing climatic conditions thunderstorms occur in the south-western Cape only rarely ('nearly five occasions per year'—Schulze 1965: 313), and although lightning is known to cause fires in this region, such fires are infrequent, especially in the coastal areas (Kruger 1979). On the other hand, since thunderstorms are a characteristic accompaniment of strong solar heating, 'lightning is about ten times more frequent' in summer-rainfall regions (Kruger 1979, quoting Kröninger 1978). This may be further evidence for summer rather than winter rainfall in the Langebaanweg area during the early Pliocene.

Another possible effect of fires and the consequent reduction in vegetation cover at this time was the exposure of the unconsolidated sediments of the region to erosion at the onset of the wet season. This would account for the large volumes of sediment carried by the river and deposited at its mouth, so building up the Varswater Formation. In addition, there was probably an increased rainfall run-off from the devegetated areas and, consequently, an increase in the volume and duration of flooding. The devastating effects of the floods would, therefore, have been intensified.

There is now some additional evidence to support the hypothesis of seasonal deposition in the PPM during flood periods. A preliminary analysis of a sample of *Sivatherium* teeth from bed 3aN suggests that it represents a 'catastrophic' rather than 'attritional' mortality (see Voorhies 1969: 46, pl. 13 (figs 1–2)). There is also a suggestion that the material in this sample was accumulated during a restricted period of the year. Since it is abundantly clear that the bed 3aN *Sivatherium* specimens were deposited in a river channel, it is almost certain that they reflect a flood-season accumulation.

The situation that resulted in many of the fossils being incorporated in the QSM and PPM is summed up below.

During the dry season terrestrial vertebrates would tend to concentrate in the immediate vicinity of the river, including the now exposed QSM floodplain, where fresh water in the generally sandy region was probably most readily available. The area adjacent to the floodplain was probably the one to which woodlands were largely confined, and was therefore the main habitat available to browsing herbivores. Towards the end of each dry season the shortage of

food for herbivores might have become acute, with fires caused by electrical storms further reducing available supplies. The fires probably killed many animals, and might have caused others to drown when they sought refuge in the river. Most affected would have been slow-moving non-swimmers such as tortoises, which are abundantly represented in the QSM.

The first heavy rains of the wet season would cause flooding of the river. If the rains fell inland and not locally, the flooding may have caught animals concentrated on the floodplain unawares and swept them downstream to be deposited at its mouth, which was then in the vicinity of the present 'E' Quarry. Animals weakened by starvation or injured by fires were less likely to escape the flooding than healthy animals. In addition to animals drowned in the flood, the river would have carried with it remains of the animals that had previously died on the floodplain. The arrival at the river mouth of large numbers of carcasses of terrestrial vertebrates must have attracted aquatic carnivores such as seals and sharks to the area, while carcasses stranded on the river-banks would have attracted terrestrial scavengers. Those that died had their remains added to the accumulating deposits.

The representation of animals in the QSM and PPM, the large numbers of individuals involved, and the condition of their remains are thus indicative of the deteriorating environment in the region during the early Pliocene. A comparison between the mammals represented then and in modern times indicates very clearly that the fauna of the region underwent a radical change in the intervening period. Evidently this change had already been initiated by the early Pliocene.

The period of deposition of the Varswater Formation was one of transition, with the local physiography, climate, vegetation and fauna all being in the process of change. Patterns established earlier during the Miocene were still in evidence, but those that were to characterize the Quaternary were already being established.

EVOLUTIONARY ASPECTS OF THE MAMMALIAN FAUNA

Dating as it does from the period near the Miocene–Pliocene boundary, it is to be expected that the fauna of the Varswater Formation would have characteristics of both the time that Kurtén (1971: 152) has termed the 'climax of the Age of Mammals' (i.e. the late Miocene), and the Quaternary, which is characterized by similarly spectacular faunas only in some tropical regions, and with progressively less diverse faunas in higher latitudes. The 'E' Quarry fauna is, indeed, of a transitional nature and, at least in terms of its mammals, it provides a record unparalleled in Africa of the final flowering of Tertiary life before the climatic instability and extremes of the Quaternary so drastically altered the character and composition of the continent's fauna.

The 'E' Quarry carnivores serve admirably to illustrate the transitional nature of the fauna. They include representatives of genera such as *Agriother-*

ium, *Plesiogulo* and *Enhydriodon*, which were characteristic of the late Tertiary over wide areas of Africa, Eurasia and North America. Similarly, the hyaenas have previously been cited as an example of a group that had maintained a pattern of representation established during the late Miocene, and which contrasted with that during the Quaternary when the family was less diverse and individual species were more highly specialized (Hendey 1978c). The larger felids from 'E' Quarry are all sabre-toothed forms, and although such forms had a long subsequent history, they were never again to predominate as they did during the late Tertiary. By contrast, the mongooses of the early Pliocene were then only in the early stages of their radiation, which was to reach a climax during the Quaternary (Hendey 1974b).

Perhaps the best single example of a species intermediate between generalized Miocene forms and highly specialized Quaternary ones was not a terrestrial species but the seal, *Homiphoca capensis* (Hendey & Repenning 1972; De Muizon & Hendey 1980). In this instance the intermediate character could be fully documented, since *H. capensis* is very well represented, and there are closely related forms still living which are both generalized (monk seals) and specialized (Antarctic seals).

The 'E' Quarry carnivores also include early ancestors of species that were to become characteristic of later carnivore faunas. For example, *Hyaena abronia* and *Mellivora benfieldi* are likely ancestors of *H. hyaena* and *M. capensis* respectively (Hendey 1978c, 1978d). It is, however, equally significant that ancestors of several important elements of the Quaternary carnivore fauna of Africa are not represented at 'E' Quarry. These elements are the lion (*Panthera leo*), leopard (*P. pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*), hunting-dog (*Lycaon pictus*), and jackals (*Canis* spp). They are largely open-country carnivores, with the cursorial cheetah being a particularly good example of an animal evolved to meet the changing environmental conditions of the late Tertiary. The cheetah has no counterparts amongst the 'E' Quarry felids, although the fauna does include an early 'hunting-hyaena' (*Euryboas*), which was an ecological vicar of the cheetah during the late Pliocene and early Pleistocene.

While the evolution of specialized carnivores such as the lion, leopard, cheetah, spotted hyaena, and hunting-dog can be ascribed ultimately to the changing environment of the late Tertiary, the reasons for the subsequent success of generalized forms such as the jackals are less obvious. The ecological vicars of the jackals in the 'E' Quarry fauna were the civets (Hendey 1974a). At least in terms of their size and dentitions there was little difference between jackals and civets and it can be assumed that they had similar feeding-habits. However, the early Pliocene civets had relatively small brains (Fig. 17), and it is possible that in terms of sight, smell, and/or hearing they were inferior to jackals and were thus unable to compete with them successfully. The living African civet that survived this competition did so by becoming a nocturnal omnivore and coincidentally increasing its brain size.

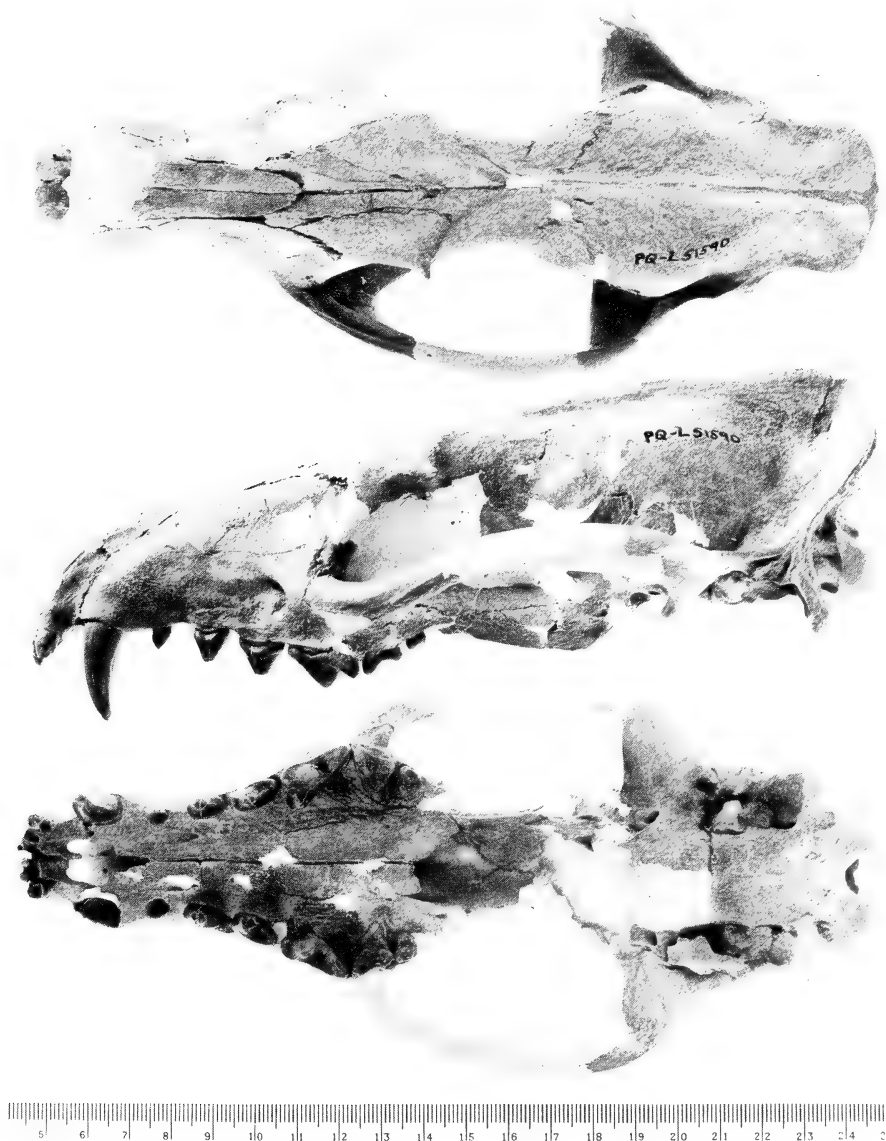


Fig. 17. Dorsal, lateral and ventral views of a civet skull (SAM-PQ-L51590) from the PPM 3aN.

In the case of the marine vertebrates such as the seal, the changing characteristics manifested in late Tertiary lineages can also be ascribed to environmental factors, principally falling sea temperatures. The development of the nutrient-rich cold upwelling in the Benguela Current System resulted not only in an adaptation in *Homiphoca* to colder conditions, but also led to adaptations in the postcranial skeleton, which permitted the more pelagic way of life required to exploit the rich off-shore food resources, and those parts of the skull connected with feeding in order to deal with the pelagic foods.

The fact that the 'E' Quarry mammals date from a period when the fauna was adapting to changing conditions has contributed to the difficulties in identifying certain taxa. In such instances the differentiation of new lineages was in its early stages, as in the case of the civets and canids (see p. 55), and consequently the distinguishing characteristics, which were later to become unequivocal, were still only slight. Apart from the examples cited above, forms that resemble one another in many respects are included amongst the mongooses (Hendey 1974a, 1974b), hyaenas (Hendey 1978c), and bovids (Gentry 1980).

The diminution of forested or wooded environments was probably the most significant factor in bringing about change amongst the terrestrial mammals. This change was manifested by extinctions, by reducing the distribution of species, and by the evolution of new taxa that were better adapted to the changed environment. Large herbivorous species must have been most affected, while the viability of carnivores which depended on them as a source of food would have been placed in jeopardy. The large bear, *Agriotherium*, falls into the latter category (Hendey 1980; 69–72). Ultimately though, the entire fauna must have been affected to some extent.

A herbivore that became extinct without issue was the woodland bos-elaphine, *Mesembriportax* (or *Miotragocerus*) *acrae*. During the late Miocene, near relatives of this bovid had been amongst the most successful and widespread of their family in Eurasia, and perhaps also Africa. Apart from the living four-horned antelope (*Tetracerus quadricornis*) and nilgai (*Boselaphus tragocamelus*) of India, the 'E' Quarry boselaphine is probably the last recorded survivor of its group.

Much the same applies in the case of the okapi-like *Palaeotragus* cf. *germaini*. Palaeotragines were an important element in the late Miocene faunas of Eurasia and Africa, but the sole survivor of the group today is the rare *Okapia johnstoni*, which is confined to forests in equatorial Africa (Churcher 1978). The Pliocene and Pleistocene history of the Palaeotraginae is poorly documented, or perhaps misinterpreted, but 'E' Quarry is one relatively late occurrence where its presence is indisputable. It is, however, a rare element in the fauna, and by the early Pliocene the heyday of the subfamily was clearly past.

Sivatherium hendeyi is the most commonly occurring of the 'E' Quarry giraffids and, although the genus survived well into the Pleistocene in Africa, it

is nowhere as commonly represented as it is in 'E' Quarry. The group to which it belonged flourished in Eurasia, and perhaps also Africa, during the late Miocene, and 'E' Quarry may provide a record of its final flowering.

There are several instances where descendants of taxa recorded from 'E' Quarry, or later related forms, had adapted to changing conditions through altering their dietary preferences. Adaptations to grazing rather than browsing were already evident in the 'E' Quarry rhinoceros (*Ceratotherium praecox*) and alcelaphines (*Damalacra acalla* and *D. neanica*), and perhaps also the buffalo (*Simatherium demissum*), gazelle (*Gazella* sp.), and neotragine (*Raphicerus paralius*). *Notochoerus*, the warthog-like descendant of *Nyanzachoerus* (Cooke & Wilkinson 1978; Harris & White 1979), was subsequently to follow suit. The 'E' Quarry grazers were still relatively primitive members of their groups, and from the stocks that they represent were to arise the characteristic grazing species which flourished in Africa during the Quaternary.

Although it was vegetational change that had the major affect on the composition of the fauna, the related factors of rainfall and temperature must also have played a role. There can be little doubt that the 'E' Quarry fauna had its origins under tropical rather than temperate conditions, and, consequently, that adaptation to cooler conditions in the terminal Miocene and early Pliocene was required. Certain of the 'E' Quarry taxa, both mammals and non-mammals, have modern counterparts only in the warmer parts of Africa, and this suggests that ultimately they did not successfully adapt to the temperate conditions that prevailed in the south-western Cape after the late Miocene. Such taxa include a snail (*Ceratophallus natalensis*), the parrots (gen. and spp not determined), the giraffe (*Giraffa* sp.), the 'okapi' (*Palaeotragus* cf. *germaini*), and the reduncines (*Kobus* spp). It is possible that even by the early Pliocene, falling temperatures had influenced the composition of the fauna, with some tropical forms having already become extinct locally (see p. 89).

The effects of a change in rainfall are not obvious. If there was indeed a change from summer to winter rainfall, this would not necessarily have had an adverse effect on the mammals, although there might have been a reaction to a lowering of rainfall and/or a lengthening of the dry season.

In assessing evolutionary aspects of the 'E' Quarry fauna, account must be taken of events elsewhere, since this fauna was as much influenced by them as it was by local environmental changes.

In the Old World the record of terrestrial life during the late Miocene is well documented in parts of Europe and Asia, but in Africa the fossil record for this period is poor. It is, however, safe to assume from the little that is known, and from earlier and later records, that Africa during the late Miocene was as richly endowed faunally as Eurasia. Its fauna was comprised of both endemic lineages and ones that had their origins in Eurasia and North America.

After a long period early in the Tertiary when it was isolated from other continents by seas and oceans, Africa-Arabia was joined to south-western Asia early in the Miocene (Berggren & Van Couvering 1974). This event had a

profound impact on the faunas of both Africa and Eurasia. Whereas earlier in the Tertiary faunal interchange had been limited to 'sweepstakes routes' (*sensu* Simpson 1967), or 'Noah's Arks' (*sensu* McKenna 1973), the early Miocene saw the opening of 'corridor routes' which allowed the first free faunal interchange in perhaps 40 million years. African emigrants to Eurasia included primates and proboscideans, while an array of Eurasian taxa, including carnivores and perissodactyls, made their appearance in Africa (Maglio 1978).

Thereafter, the corridors between Eurasia and Africa were restricted or closed intermittently, and Africa's faunal history was punctuated by periods of isolation which were interrupted by new periods of immigration. In spite of the closer connection with Eurasia, immigrant lineages to Africa evolved taxa that were usually in some respects distinct from their Eurasian counterparts, and they, together with representatives of endemic lineages, gave the African fauna a largely distinctive character throughout the later Cenozoic.

The 'E' Quarry fauna, and others of late Miocene and early Pliocene age elsewhere in Africa, provide evidence for a period of immigration from Eurasia during the late Miocene. Conversely, there is evidence from Eurasia of the immigration of African mammals at this time. For example, Azzaroli (1975: 69) concluded that it is 'firmly established that interchange of terrestrial mammals between southern and northern shores of the Mediterranean took place some time around 6,5 m.y. ago or shortly later'.

Amongst those mammals from 'E' Quarry with a late Miocene Eurasian connection is the bear, *Agriotherium africanum* (Hendey 1980). A slightly earlier member of the lineage which includes *A. africanum* is recorded from c. 6 Ma deposits at Sahabi in Libya (Boaz *et al.* 1979), and it is likely that the earliest African representative of the group entered the continent about that time or slightly earlier, that is, during the c. 6,5 Ma faunal interchange recorded by Azzaroli (1975). Other likely immigrants to Africa at this time are the hyaenids, *Ictitherium*, *Palhyaena* (= *Hyaena*), and *Hyaenictitherium*; the wolverine, *Plesiogulo*; and the false sabre-toothed cat, *Dinofelis*, the latter being a descendant of Eurasian *Metailurus* (see Hendey 1974a, 1978c, 1978d, 1980). The largest of the 'E' Quarry hyaenids, '*Adcrocuta*' *australis*, was previously thought to be included in this category, having been descended from Eurasian *Adcrocuta eximia*, but it now seems likely that these two species had a common ancestor in an earlier African *percrocuta*.

Immigrants amongst the herbivores are less obvious. One possibility is the boselaphine, *Mesembriportax* (or *Miotragocerus*) *acrae*. According to one interpretation, this species was descended from the widespread *Miotragocerus* of the Eurasian late Miocene, again with an intermediate form being recorded from Sahabi (Thomas 1979). On the other hand, it may represent an endemic African lineage that had its origins with the middle Miocene *Protragocerus*, and which evolved in parallel with Eurasian *Miotragocerus* (Gentry 1974, 1980).

It is significant that descendants of late Miocene immigrants are most obvious amongst the larger Carnivora. Such animals are less affected than

herbivores by environmental factors, and are thus capable of more rapid dispersal, while individual species tend to have wider distributions. Consequently, descendants of late Miocene immigrant carnivores to Africa might have become established in the far south of the continent sooner than their herbivorous counterparts. The more slowly dispersed herbivores are also likely to undergo more rapid evolutionary changes as they adapted to new environmental conditions, and their relationships to pre-existing forms may therefore be more difficult to determine.

Not all the ancestors of Eurasian immigrants represented in the 'E' Quarry fauna reached Africa late in the Miocene. One obvious exception is *Hipparion*, whose appearance in Africa dates back about 12.5 Ma (Churcher & Richardson 1978). By the end of the Miocene endemic African species of *Hipparion* had evolved (Churcher & Richardson 1978). The Langebaanweg *Hipparion* is of particular interest, since it is recorded from all the main fossil-bearing horizons of the Varswater Formation, as well as from younger deposits. At least one lineage (*H. cf. baardi*-*H. baardi*) is represented which is distinct not only from its counterparts in Eurasia, but also those elsewhere in Africa. The same apparently applies in the case of the two alcelaphines from 'E' Quarry, one of which has a descendant form in Baard's Quarry, although in this instance the origins of the group are still obscure (Gentry 1980).

Another of the 'E' Quarry species that might have been descended from an Eurasian middle Miocene species is the peccary, *Pecarichoerus? africanus*. Previously a connection with the Asian *Pecarichoerus orientalis* was suggested (Hendey 1976b), but a recently described peccary from the late Vindobonian of Spain, *Barberahyus castellensis* (Golpe-Posse 1977), is remarkably similar to the 'E' Quarry species and they may have a close phylogenetic relationship, with descendants of the Spanish form having entered Africa at the same time as *Hipparion*.

In interpreting the evolutionary history of Varswater Formation mammals it is therefore necessary to take into account the following possibilities:

1. Species represent lineages endemic to Africa.
2. Species represent lineages of Eurasiatic origin, and with a long history in Africa.
3. Species represent lineages of Eurasiatic origin, and with only a short history in Africa.
4. Species represent lineages of African or Eurasian origin, but which are endemic to the southerly parts of the continent.

In addition, account must be taken of the possibilities that certain lineages represented elsewhere in Africa failed to make an appearance in the Langebaanweg area, only arrived there long after they were established further north, and became extinct there earlier, or survived later, than they did further north.

The matter of locally endemic species, non-arrivals, late arrivals, early extinctions, and late survivors during any given period depends on local

environmental conditions, as well as the degree to which the south-western Cape, or southern Africa, was zoogeographically isolated from regions further north. The potential for isolation of the south-western Cape, largely by a barrier of aridity or semi-aridity, has already been established (Hendey 1974a; 14–19), although the degree of isolation at various times in the past is difficult or impossible to determine. This applies particularly to pre-Quaternary times, when African environments were very different from those of the present, and when the fossil record is generally poor.

The fact that 'E' Quarry species such as *Hipparion* cf. *baardi* and the two alcelaphines are, or may be, different from contemporary counterparts further north in Africa, suggests that the south-western Cape, or an even larger area of southern Africa, had been zoogeographically isolated some time during the late Miocene. On the other hand, this isolation could not have been complete, or had broken down very late in the Miocene, since there evidently had been some immigration of taxa shortly before deposition of the QSM and PPM. Such taxa include *Agriotherium* and the others referred to above.

Since the Varswater Formation was laid down over an appreciable period, it is also possible that during this period some species arrived in the area as immigrants, while others became extinct. However, it may not be possible to determine that this actually happened. The simple fact that certain species are not recorded low in the sequence does not necessarily mean that they were not present in the area. In other words, the first appearance of a species in the sequence was not necessarily coincident with its first appearance in the region. Conversely, the presence of certain taxa low in the sequence, and their absence higher up, is not necessarily indicative of their extinction. Both sampling inadequacies and taphonomic factors are potential biases in the 'E' Quarry record.

Sampling inadequacies is the less serious problem, since the sample sizes from the QSM, bed 3aS, and bed 3aN are large. Nevertheless, past experiences at this locality have shown that it is a factor that cannot be dismissed. For example, it was once thought that porcupines had not been an element of the fauna (Hendey 1974a), but remains of a single individual were subsequently found in the QSM (Hendey 1976a), and since then fragmentary remains of a second species have turned up on several occasions in beds 3aS and 3aN.

The problem with taphonomic factors is that the environments of deposition of the various elements in the succession vary, and it is obvious that taxa represented in one (e.g. river floodplain) may differ from those in another (e.g. river channel).

The QSM assemblage largely represents the remains of animals that lived and died in the immediate vicinity, whereas the beds 3aS and 3aN assemblages are largely comprised of animal remains washed in by the river from elsewhere. Consequently, the presence of species in these two sets of deposits simply reflects the opportunity for their remains to reach their points of deposition, and may have nothing to do with their presence or absence in the region.

Individual taxa must, however, be assessed separately. For example, the fact that hippos are not recorded from the QSM may be due to the lack of exposures of those deposits where their remains were most likely to be preserved, that is, those of the main river channel of that time. However, even in the recorded channel deposits hippos are unequally represented. They were extremely rare in bed 3aS, whereas they were much more common in bed 3aN. It is thus possible that the representation of this animal in the 'E' Quarry sequence is a true reflection of its initial absence (i.e. in QSM times), and its subsequent presence in increasing numbers (i.e. in beds 3aS and 3aN).

The occurrence of the giant pig, *Nyanzachoerus*, is in curious contrast to that of the hippo. *Nyanzachoerus* occurs quite commonly in the QSM, *N. cf. pattersoni* being one of the characteristic species of this horizon. This species may also be present in bed 3aS, although it is extremely rare. A second species, *N. cf. jaegeri*, is definitely recorded from bed 3aS, although it, too, is uncommon. However, neither species, nor any other pig, is recorded from bed 3aN. This creates the impression that *Nyanzachoerus* was 'replaced' locally by the hippo. There is, however, no evidence from elsewhere that hippos and *Nyanzachoerus* were mutually exclusive taxa, although they might well have competed for a common food source.

The situation in respect of these animals at Langebaanweg might have differed from that in areas where they did co-exist. Since the local environment was deteriorating during the early Pliocene, it is possible that competition between hippos and *Nyanzachoerus* for diminishing food resources was critical enough to cause the extinction of the latter. Thus the record of hippos in bed 3aS may, indeed, coincide with the first appearance of these animals in the Langebaanweg area and the initiation of competition with *Nyanzachoerus*, the latter process being concluded in the favour of the hippos by the time that bed 3aN was deposited. Alternatively, the two forms might have co-existed throughout the period of deposition of the QSM and bed 3aS, with the displacement process being more gradual. The first of these alternatives is perhaps the more likely in view of the observed relative abundance of the two forms.

One of the more intriguing features of the QSM and PPM faunas is the extreme rarity of primates in the former and their complete absence in the latter. Of the many thousands of mammalian teeth recovered to date, there are only two specimens from the QSM identified as primate, while there are no primate bones amongst the far more numerous identified postcranial remains from the QSM and PPM. Primates are clearly grossly under-represented in the 'E' Quarry fauna, given its location in Africa, the great number and variety of mammals recorded, and the vast number of specimens already collected and identified. In older and broadly contemporary faunas elsewhere in Africa, and in southern Eurasia, both terrestrial and arboreal primates are represented, sometimes in appreciable numbers and variety and often in assemblages far smaller than that from 'E' Quarry.

It was suggested elsewhere that the location of Langebaanweg on the coast

in the far south of the continent might have had a bearing on the under-representation of primates (Hendey 1976a: 234). The coastal situation is unlikely to have been significant, since primates are not necessarily averse to this kind of environment, either now or in the past. For example, the broadly contemporary fauna from Montpellier, which was accumulated in a similar environment, includes primates (see below).

The situation of Langebaanweg at nearly 34°S may be a more significant factor. Over 80 per cent of Africa's non-hominid primates occur in low latitudes, between 15°N and 15°S (see distribution maps in Dorst & Dandelot 1970), and are thus most characteristic of the hot tropical regions. In the warm-temperate south-western Cape there is only one non-hominid primate recorded, which is about 2 per cent of the total in the Ethiopian Region. This species is the chacma baboon, *Papio ursinus*. A monkey (probably *Cercopithecus*) is tentatively recorded on the basis of early historical records. The Pleistocene fossil record for the south-western Cape is comparatively good, but once again only one non-hominid primate is recorded, i.e. the baboon, *Theropithecus oswaldi*, from the middle Pleistocene of Elandsfontein. Clearly, the frequency in the occurrence of primates can be correlated with latitude, and, consequently, also with temperature.

However, the lower temperatures of higher latitudes do not necessarily directly limit the occurrence of primates. Instead, they have the effect of limiting the food resources available to essentially herbivorous primates. Tropical regions remain productive in terms of such food resources throughout the year, but in temperate regions they are readily available only during summer. Consequently, although the vegetation at Langebaanweg during the early Pliocene was such that the occurrence of both terrestrial and arboreal primates might have been expected, winter temperatures were probably already too low to have maintained adequate food supplies for most primates. This order may, therefore, be included in the hypothetical group of animals that became extinct in the south-western Cape earlier than elsewhere (see p. 83).

It is worth noting that primates were still present in contemporary faunas of comparable latitudes in the Northern hemisphere. This is readily explained by the fact that the existing zonality in world climates had yet to be established. The glaciation of the Arctic lagged behind that of Antarctica, and it was not until about 3 Ma that the situation in the two hemispheres was more or less equalized.

The above theory implies that primates were still present in the far south of the continent during the warmer period in the late Miocene and earlier. However, although the Miocene mammal record for southern Africa is very poor, it may again be significant that this record includes no primates. Only one Miocene occurrence is presently known where the assemblage is sufficiently large for primates to have been expected. It is from Arrisdrift in the southern Namib desert, and in this instance it was suggested that zoogeographic barriers between east and southern Africa might have impeded the southward dispersal of primates (Hendey 1978b: 35).

Other notable absentees from the 'E' Quarry fauna are the Deinotheriidae, Chalicotheriidae, and, amongst the non-mammals, the Crocodilia. Proboscideans are a comparatively rare element in this fauna, and the absence of a deinotheres may therefore reflect a sampling deficiency. The same may apply in the case of the chalicotheres, an animal that was uncommon elsewhere in Africa as well. The situation in respect of the Crocodilia is likely to be different, since wherever these animals are present they are likely to be well represented at least by isolated teeth and scutes, if not by other skull parts and postcranial bones. Crocodiles have not been recorded from any other south-western Cape deposits either, and their absence is probably due to the relatively low temperatures in local aquatic environments in post-Miocene times.

Both deinotheres and crocodiles are recorded from the early middle Miocene deposits at Arrisdrift, 500 km to the north, so they, like primates, might have had their ranges restricted by falling temperatures in the far south of the continent during the late Miocene and early Pliocene.

Although the 'E' Quarry fauna includes Eurasian immigrants, it was dominated by taxa that were, and, in some cases, still are, characteristically 'African'. These include groups such as the Macroscelididae, Chrysokloridae, Tubulidentata, Proboscidea, Hyracoidea, and certain tribes of Bovidae.

The 'African' character of this fauna is clearly manifested by a comparison with the broadly contemporary Montpellier fauna (Table 9). Apart from these faunas being of comparable age, they are from similar coastal situations. In their overall composition the faunas of 'E' Quarry and Montpellier are remarkably alike, comprising of a similar array of carnivores, proboscideans, perissodactyls, artiodactyls, cetaceans, and some smaller mammals. The latter are under-represented at Montpellier probably because of sampling deficiencies, while the under-representation of primates in 'E' Quarry is ascribed to the climatic factors discussed above.

In spite of their overall similarities, the two faunas are taxonomically distinct, the differences being mainly at generic and specific level. Conspicuity, or very close relationship, is largely confined to the Carnivora, for reasons discussed earlier (see p. 84), but even in this group there are obvious differences.

The most striking and unexpected of these differences is the absence of hyaenas at Montpellier. Hyaenas are well represented in Europe at localities of late Miocene and Pleistocene age, and they are also common in 'E' Quarry. Their comparative rarity (or absence) at European localities of early Pliocene age has yet to be satisfactorily explained. Smaller viverrids are also not recorded at Montpellier, but otherwise differences from 'E' Quarry carnivores are at generic or specific level.

For example, the badgers represent the genera that are still characteristic of the continents concerned (i.e. *Mellivora* in Africa, *Meles* in Europe). Similarly, the seals, both of which belong to the subfamily Monachinae, are most closely related to taxa that are still found in geographical proximity (i.e. *Homophoca* to Antarctic Lobodontini, *Pristiphoca* to Mediterranean *Monachus monachus*).

TABLE 9

The mammalian faunas of the Varswater Formation (QSM and PPM), Langebaanweg, and the Pliocene deposits at Montpellier, France.

	LANGEBAANWEG	MONTPELLIER*
Insectivora and Chiroptera	Present	Not recorded
Primates	1 species	3 species
Pholidota and Tubulidentata	Present	Not recorded
Carnivora		
Canidae . . .	2 species	Not recorded
Ursidae . . .	<i>Agriotherium africanum</i> (aff. <i>insigne</i>)	<i>Agriotherium insigne</i>
Mustelidae . . .	<i>Plesiogulo monspessulanus</i> <i>Mellivora benfieldi</i> <i>Enhydriodon africanus</i>	<i>Plesiogulo monspessulanus</i> <i>Meles gennevauxi</i> <i>Lutra affinis</i>
Phocidae . . .	<i>Homiphoca capensis</i>	<i>Pristiphoca occitana</i>
Viverridae . . .	<i>'Viverra' leakeyi</i> Viverrinae sp. B	<i>Viverra</i> aff. <i>pepratxi</i>
	Genetta and Herpestinae	Not recorded
Hyaenidae . . .	Several species	Not recorded
Felidae . . .	Machairodontinae (2 spp) <i>Felis</i> aff. <i>issiodorensis</i> (? aff. <i>christoli</i>)	Machairodontinae (1 sp.) <i>Felis christoli</i>
	Other Felinae (3 spp)	Not recorded
Proboscidea . . .	<i>Mammuthus subplanifrons</i> <i>Anancus</i> sp.	<i>Mastodon arvernensis</i>
Hyracoidea . . .	<i>Procavia</i> cf. <i>antiqua</i>	<i>Pliohyrax occidentalis</i>
Perissodactyla		
Equidae . . .	<i>Hipparion</i> cf. <i>baardi</i>	<i>Hipparion crassum</i>
Rhinocerotidae . . .	<i>Ceratotherium praecox</i>	<i>Dicerorhinus megarhinus</i>
Tapiridae . . .	Not recorded	<i>Tapirus arvernensis</i>
Artiodactyla		
Tayassuidae . . .	1 species	Not recorded
Suidae . . .	<i>Nyanzachoerus</i> (2 spp)	<i>Sus arvernensis</i>
Hippopotamidae . . .	1 species	Not recorded
Giraffidae . . .	3 species	Not recorded
Cervidae . . .	Not recorded	3 species
Bovidae . . .	12 species, including a <i>Gazella</i> sp.	2 or 3 species, including a <i>Gazella</i> sp.
Lagomorpha . . .	<i>Pronolagus</i> sp.	<i>Prolagus</i> sp.
Rodentia . . .	Many species	1 species
Cetacea . . .	Several species	Several species

*Anonymous 1975

Amongst the non-carnivores, giraffids and bovids are the predominant ungulates in 'E' Quarry, whereas at Montpellier giraffids are absent (or not recorded), and cervids are present in addition to bovids. *Hipparion* is recorded at both localities. The combinations of Bovidae–Giraffidae–Equidae in 'E' Quarry and Cervidae–Bovidae–Equidae at Montpellier are still characteristic of the continents concerned.

DATING OF THE LANGEBAANWEG SUCCESSION

One of the most persistent problems pertaining to the Varswater Formation is that of its age. As is frequently the case in southern Africa with deposits of late Cenozoic age, only indirect dating methods can be used. The situation is, however, exceptional in that in this instance faunal, botanical and geological evidence is actually or potentially available for relative dating purposes. The present study has clarified the dating problem.

Hitherto dating has depended largely on the fossil mammals of the Varswater Formation. Initially these fossils were thought to be of early Pleistocene age (e.g. Singer 1961; Boné & Singer 1965; Hendey 1969, 1970a), but subsequently it was suggested that the formation included both Pliocene and Pleistocene elements (Hendey 1970b). This is, indeed, the case with the fossil assemblage from Baard's Quarry (Hendey 1978a), but the Varswater Formation in 'E' Quarry is entirely of late Tertiary age. This was established with the realization that geological evidence had been misinterpreted, that some of the mammalian taxa represented had been misidentified, and that the provenance of an *Equus* tooth had been incorrectly recorded (Hendey 1972b). Thereafter, the most widely accepted age estimate was early Pliocene (c. 4–5 Ma) (e.g. Hendey 1973, 1974a). Instead of resolving the issue, more recent faunal studies have provided contradictory dating evidence and have also indicated that deposition of the Varswater Formation took place over a prolonged period (e.g. Hendey 1976a, 1978d, 1980). As a result, when referring to the age of this formation it has been the practice to give only the outside age limits, which are 7 and 3.5 Ma. These limits include the terminal Miocene as well as the early Pliocene.

The principal difficulty with faunal dating has been that broadly contemporary faunas elsewhere in Africa, some of which are securely dated by absolute age determinations, are not well known. Consequently, the basis for comparison is far less than the lengthy 'E' Quarry faunal list would suggest. In addition, the location of Langebaanweg near the southern continental extremity raises the problem of regional peculiarities in the fauna of the kind discussed above (see pp. 85–89).

In that discussion the 'E' Quarry hippo was used as an example to illustrate a point, and it can be used again to indicate the kind of difficulties that arise in faunal dating. The fossil record of Hippopotamidae in east Africa is good, and the evolutionary history of the family is well understood (Coryndon 1978). Hippos are not the best mammals to use for relative dating purposes, since they are conservative animals in an evolutionary sense, and are difficult to identify

to species level on the basis of fragmentary material. Nevertheless, they may serve as age indicators in the case of faunas such as the one from 'E' Quarry.

It was suggested earlier that hippos might have made their appearance in the Langebaanweg area only during the period of deposition of bed 3aS (or shortly before). Hippos are first recorded in east Africa as early as 10 Ma (Coryndon 1978), but it would be unwise to conclude that their first appearance there coincided with their appearance in the Varswater Formation. It is much more likely that environmental factors retarded the southward dispersal of this water-demanding animal, perhaps for an appreciable period. Hippos may thus be an example where geography is a complicating factor when they are used for relative dating purposes.

A contrasting example of a herbivore noted for its rapid dispersal and utility in faunal dating is that of *Hipparion*, the three-toed horse that first made its appearance in Africa at about 12,5 Ma, and which survived on this continent well into the Pleistocene (Churcher & Richardson 1978). Again there is a complicating factor with the Langebaanweg representatives of this genus. The most commonly occurring of the 'E' Quarry species is *Hipparion* cf. *baardi*, which evidently belongs on a lineage endemic to the more southerly parts of Africa, and comparisons with broadly contemporaneous *Hipparion* elsewhere in Africa, therefore, provide little evidence of their likely relative age.

The Langebaanweg *Hipparion* has, however, provided useful relative age information on deposits occurring in the immediate vicinity. For example, the GM *H.* cf. *primigenium* is consistent with the late Miocene date for this horizon deduced on other evidence (see p. 23). Another species, *H.* cf. *namaquense*, is known only from the uppermost levels of the Varswater Formation, and may even come from overlying deposits (Hendey 1976a; Hooijer 1976). Finally, the Baard's Quarry *H. baardi*, which is now also recorded from the Anyskop terrestrial deposits, is clearly distinct from the 'E' Quarry *H.* cf. *baardi*, and suggests a younger date for the deposits in which it occurs (Hendy 1978a; see also p. 38).

Bearing in mind the difficulties in long-range correlations suggested by the hippo and *Hipparion*, and the other potential regional peculiarities discussed earlier, it is evident that in faunal dating of the Varswater Formation the following two factors are of the greatest significance:

1. The occurrence at more securely dated localities of species conspecific with ones occurring in 'E' Quarry.
2. The evolutionary state of 'E' Quarry taxa relative to those of related taxa from dated localities elsewhere.

Initially it was two species from the QSM that were at the core of the correlations indicating an early Pliocene age. They were the elephant, *Mammuthus subplanifrons*, and the pig, *Nyanzachoerus* cf. *pattersoni* (or *kanamensis*). A 5 Ma maximum age for the QSM was based on the belief that counterparts of

these two species in the Lothagam 1 fauna from Kenya were aged between 5 and 6 Ma (Patterson *et al.* 1970; Maglio 1973). Subsequently Hooijer & Maglio (1974: 4) concluded that this fauna 'may be somewhat older than [6 Ma, but] it is not likely to be much younger'. Behrensmeyer (1976: 167) noted that it is 'obviously important to think of the Lothagam 1 fauna as representative of a relatively long time span' and that 'the fauna from 1C may be somewhat younger than 6,0 m.y.' The base of the Lothagam sequence is underlain by volcanics dated at 8,3 Ma (Behrensmeyer 1976), which is, therefore, the absolute maximum age of the Lothagam fauna.

Although there is still uncertainty about the actual age of the Lothagam 1 fossils, there can be virtually no doubt that they pre-date those from the QSM, and, consequently, also those from beds 3aS and 3aN. The Lothagam 1 elephants (*Stegotetrabelodon orbus*, *Primelephas gomphotheroides*) and the pig (*Nyanzachoerus tulotus*) are more primitive than their counterparts from 'E' Quarry, as is an undescribed hyaenid from Lothagam 1.

On the other hand, the c. 4 Ma fauna from Kanapoi, 75 km south of Lothagam (Behrensmeyer 1976), is apparently younger than that from 'E' Quarry, although the evidence for this is more slender. An undescribed hyaenid from Kanapoi is certainly more advanced than its counterparts in the 'E' Quarry 'Hyaena group' (see Hendey 1978c). The presence of the pig, *Notochoerus*, at Kanapoi and its absence in 'E' Quarry is also indicative of a younger age for the former. In addition, the QSM *Nyanzachoerus* cf. *pattersoni* is slightly more primitive than the *N. pattersoni* from Kanapoi in retaining P¹. The preceding evidence indicates that the age difference between the two faunas is of no great magnitude, an opinion supported by the fact that their elephants are in a comparable evolutionary state (Maglio 1973).

There is, however, a complication with the *Nyanzachoerus* cf. *jaegeri* from bed 3aS in 'E' Quarry. White & Harris (1977) and Harris & White (1979) have suggested that the relative stratigraphic positions of *N.* cf. *pattersoni* (or *kanamensis*) and *N.* cf. *jaegeri* in 'E' Quarry are evidence in support of their theory that the latter evolved from the former. According to their correlation the upper levels of the Varswater Formation (i.e. beds 3aS and 3aN) actually overlap with the Kanapoi Formation (Harris & White 1979, fig. 134). This conclusion is in conflict with the evidence that suggests that all of the Varswater Formation is older.*

The most positive indication of the earlier date for the Varswater Formation relative to the Kanapoi Formation comes from the hyaenids. The three 'E' Quarry species most closely related to the Kanapoi hyaenid are *Ictitherium preforfex*, *Hyaena abronia*, and *Hyaenictitherium namaquense*, all of which retain P₁ and M₂, teeth which the Kanapoi species has lost.

* A recent examination of the 'E' Quarry *N.* cf. *jaegeri* by T. D. White has led him to believe that it represents a more primitive variety than the one from Kanapoi, and that the 'E' Quarry pigs are consistent with a 5 Ma date.

Correlation of the 'E' Quarry fossils with those from east African localities such as Lothagam and Kanapoi was recently further complicated by Gentry's (1980: 333) conclusion that 'the bovids best indicate an age of about 6 m.y. for the fauna'. The bovids thus suggest an age comparable to Lothagam 1, and appreciably older than Kanapoi. However, the bovids do not necessarily rule out a younger age, and at least in the case of the buffalo, *Simatherium demissum*, are consistent with such an age. Gentry (1980: 332) found that '*Parabos boodon*, which is at a comparable evolutionary level [to *S. demissum*, but] on a different lineage, comes from Perpignan, which is given an age of about 4,8 m.y.'

While the utility of groups such as the elephants, pigs, and bovids in faunal dating is undeniable, preference is here given to that of the carnivores. The environmental tolerance of these animals allows at least the larger species to disperse rapidly when the opportunity arises, with little or no evolutionary adaptation necessarily required, and with consequent wide distributions for individual species. This facilitates long-distance correlations. The post-Lothagam 1 and pre-Kanapoi age for the 'E' Quarry fauna indicated by the hyaenids is, therefore, regarded here as more acceptable than the conflicting evidence of the pigs and bovids, and the equivocal evidence of the elephants. The outside age limits of 3,5 and 7 Ma are thus reduced to 4 and 6 Ma, with a median estimate of 5 Ma applying.

The 'E' Quarry carnivores provide further evidence in support of the 5 Ma estimate. The recent study of the *Agriotherium* from this locality suggested that it is at a comparable evolutionary stage, or, in the case of the bed 3aN material, perhaps even slightly more advanced than the *Agriotherium* from Montpellier in France. Similarly, available materials of the *Plesiogulo* and a small *Felis* from the two localities are virtually indistinguishable. Other, more general similarities between the two faunas were referred to earlier (see p. 89, Table 9), and faunal evidence thus points to broad contemporaneity between the 'E' Quarry deposits and those of Pliocene age at Montpellier.

The latter were laid down during the marine transgression that terminated the Messinian salinity crisis and ushered in the Pliocene. It was this correlation that first suggested that deposits in the Langebaanweg area could be related to global phenomena of the late Tertiary, and which prompted the re-examination of the local succession, a process that was to culminate with the correlation with global sea-level changes (see pp. 12–18, Fig. 3, Table 2).

This correlation has placed the matter of the age of individual elements in the Langebaanweg succession in an entirely new light. Whereas previously even correlations with deposits and faunas elsewhere in Africa were generally tentative, there is now the potential for secure correlations with successions recorded from all the continents and oceans of the world. In addition, the Langebaanweg area could become the key to interpreting other late Tertiary strata in southern Africa, which have often proved difficult to date, and which have had obscure histories and relationships.

While the correlation of individual elements in the Langebaanweg succes-

sion with subdivisions of the late Tertiary epochs appears secure, the absolute or chronometric ages of these elements have yet to be precisely determined.

For example, although the QSM, PPM, and Anyskop marine deposits date from the early Pliocene transgression, there is as yet no consensus on the timing and duration of this event. On the basis of evidence from the Mediterranean Basin, Van Couvering *et al.* (1976) and Van Couvering & Berggren (1977) indicate that this transgression took place between 5.0 and 4.5 Ma, whereas Vail & Hardenbol (1979) indicate it as a rapid event that took place at 5.2 Ma. The essential difference between these interpretations concerns the dating of the Miocene–Pliocene boundary, which is taken respectively at 5.0 and 5.2 Ma, while there are also implications concerning the duration of the transgression.

Clearly, the dating of the Miocene–Pliocene boundary is a matter that cannot be resolved on the basis of evidence from Langebaanweg. There is, however, little doubt that a generally acceptable date, probably 5.2 Ma (see Van Couvering 1978), will result from the many investigations relevant to this question. The same applies in the case of the duration of the early Pliocene transgression. Judging from evolutionary changes manifested in certain mammalian taxa common to more than one level of the QSM and PPM (see p. 24), the phase of the transgression represented by these deposits might have been in the order of many millennia, while the transgression as a whole could conceivably have lasted several hundred thousand years.

Until these issues are resolved, it will be convenient to use the 5 Ma estimate suggested above in reference to the deposits in the Langebaanweg area that date from the early Pliocene transgression (i.e. the QSM, PPM and Anyskop marine deposits).

There are more marked differences of opinion over the dating of the Pliocene–Pleistocene boundary, and these have a bearing on the inferred chronometric dates of the later elements in the Langebaanweg succession, particularly the Baard's Quarry fluviatile deposits. In recent years it has become common practice to date the Pliocene–Pleistocene boundary at either 1.8 Ma (e.g. Berggren & Van Couvering 1974), or 1.6 Ma (Haq *et al.* 1977). A contrasting opinion is that of Vail & Hardenbol (1979), who fixed this boundary at 2.8 Ma, which coincides with the termination of their sea-level cycle, TP3.

It was with an age range of 2–3 Ma in mind that the age of the Baard's Quarry fluviatile deposits fauna was suggested to be late Pliocene/early Pleistocene. It now appears that at least a part of this fauna is younger than 2 Ma, a conclusion that is based on the presence of *Equus*. According to Lindsay *et al.* (1980: 135) 'there were at least three major dispersal events of large mammals during the Pliocene (at 1.9, 2.6 and 3.7 Myr)', with *Equus* having dispersed into Africa during the 1.9 Ma event. The Baard's Quarry fluviatile deposits, therefore, cannot be older than 1.9 Ma, and are more likely to date from sea-level cycle QI than cycle TP3 (see p. 41).

This raises another problem concerning the fauna of these deposits. There are other elements in the assemblage that would be more consistent with an age

of more than 2 Ma. This was discussed by Hendey (1978a) and Gentry (1980), and it now seems that the possible temporal heterogeneity of this fauna was dismissed too lightly in the former study. The composition of this fauna can be most readily explained by the hypothesis that while the deposits themselves date from cycle Q1, they include both contemporary fossils and others reworked from pre-existing Pliocene deposits.

There are thus several issues relating to the age of the post-Varswater Formation deposits in the Langebaanweg area that have yet to be settled, while the chronometric ages of all elements in the succession have also to be established. In addition, Vail & Hardenbol (1979: 79) concede that there 'is no question that considerably more research needs to be undertaken to document the magnitudes and timing of eustatic sea-level changes'. Nevertheless, little significance is attached to the present uncertainties concerning details of the Laangebaanweg succession and global sea-level changes. The agreement between them is sufficient to justify the conclusion that the former can for the most part be regarded as securely dated in a geological sense. At the very least, there is now a sound basis on which future research on dating can be based.

In conclusion, it should be mentioned that botanical evidence of age is potentially available for certain elements in the succession, although for the present and in the immediate future the faunal and geological dating of the Langebaanweg sequence will provide data for palaeobotanical studies. A tentative 'Pollen Zone' sequence for the south-western Cape has already been established (Coetzee 1978), and there is apparently considerable potential for refining this scheme (J. A. Coetzee, pers. comm.). The existing pollen sequence is only tentatively correlated with the 'E' Quarry succession (Table 8).

SUMMARY AND CONCLUSIONS

Cenozoic deposits in the vicinity of Langebaanweg are comprised largely of a late Tertiary succession of clastic sediments. They include economically important phosphate deposits and some immensely rich fossil occurrences. The history of this succession has been reinterpreted on the basis of geological and palaeontological evidence, and it has been correlated with the record of South African west coast sea-level changes, for which successive shorelines at 30 m, 90 m, 50 m and 20 m above present sea-level are recognized. This interpretation is in accord with the global sea-level changes recorded by Vail & Hardenbol (1979).

The succession is as follows:

1. Basal element ('pre-GM deposits')—early to middle Miocene transgression (part of global sea-level cycles TM1.3, TM1.4, TM2.1 and TM2.2); terrestrial and marine complex.
2. No local record—middle to late Miocene regression (cycle TM2.3).
3. Gravel Member (GM) of the Varswater Formation—late Miocene regression (30 m shoreline—cycle TM3.1); marine beach complex.
4. No local record—terminal Miocene regression (cycles TM3.2, TM3.3).

5. Quartzose Sand Member (QSM) of the Varwater Formation—early Pliocene transgression (cycle TP1); estuarine complex with floodplain (QSM I), salt marsh (QSM II) and tidal flat (QSM III) facies.
6. Pelletal Phosphorite Member (PPM) of the Varwater Formation—early Pliocene transgression (cycle TP1); fluvatile (beds 3aS and 3aN) and marine littoral (PPM undifferentiated) complex.
7. Anyskop marine deposits—early Pliocene transgression (cycle TP1); coastal barrier complex.
8. Marine platform south-east of Langebaanweg—early Pliocene transgression (90 m shoreline—cycle TP1).
9. Anyskop terrestrial deposits—late Pliocene regression (50 m shoreline—cycle TP2).
10. Baard's Quarry fluvatile deposits—late Pliocene regression, or, more probably, early Pleistocene transgression (20 m shoreline—cycle TP3 or cycle Q1).

The local succession is completed by Quaternary deposits, including a nearly ubiquitous covering of aeolian sands. The area also has fossil occurrences and hominid occupation sites dating from the middle Pleistocene, late Pleistocene, and Holocene.

The nature of this succession was determined by the physical geography of the region, while the preservation of an unusually large body of early Pliocene sediment was due to the development of a coastal barrier complex, part of which survived subsequent erosion, and which protected underlying deposits.

Palaeontological investigations have centred on the Varwater Formation as it is exposed in an open-cast phosphate mine, 'E' Quarry. Some plant fossils are represented in these and underlying deposits, while about 230 invertebrate and vertebrate taxa, ranging from protozoans to mammals, have been recorded, mainly from the QSM and PPM. The fossils were recovered from a variety of marine, freshwater and terrestrial depositional environments. The species and body part representation, and the condition of specimens, was dependent on the source of the material.

Most of the collected invertebrates have been described, but the lower vertebrates are still largely unstudied. The birds evidently represent the largest pre-Pleistocene assemblage known anywhere, and they are also largely unstudied. The mammals are the most intensively studied and best represented group, although only about half of the eighty species recognized have been described. They range from shrews and mice to elephants and whales, and those already studied include four new genera and sixteen new species.

Detailed analyses of assemblages from the various depositional environments have yet to be undertaken. However, preliminary observations have revealed evidence for both subaerial and subaqueous deposition of material (e.g. in QSM 1, and in PPM, 3aN respectively). Individual specimens show signs of damage by such processes as carnivore activity (e.g. toothmarks, etching by stomach acids) and fires.

Late Tertiary environments contrast sharply with that of the present, which is semi-arid (summer dry/winter wet), with no naturally occurring surface freshwater, and with a rather sparse sclerophyll (fynbos) vegetation without indigenous trees. During the Miocene, tropical forests, possibly associated with a monsoon climate, existed in the area, but by the early Pliocene the environment was deteriorating. Temperatures had moderated from tropical to temperate, while precipitation had probably declined. Rainfall was then strongly seasonal, with a summer-wet/winter-dry pattern being likely. Wooded areas were probably restricted to the immediate vicinity of the river which was responsible for feeding in most of the sediment comprising the QSM and PPM. Grazing species amongst the mammalian herbivores indicate the presence of grasslands, and there is palynological evidence for the presence of fynbos vegetation types. However, woodland browsers still formed a significant element in the mammalian fauna, although dental abnormalities indicate stresses in these populations which might have been due to the diminution of suitable habitats, and aggravated by factors such as droughts and fires.

The evidence for changing environments at Langebaanweg during the late Tertiary is in keeping with the record elsewhere in the world. This contributed to the correlation of the local succession with others elsewhere in the world (e.g. the Mediterranean Basin), which were also under the influence of such phenomena as changes in the volume of the Antarctic ice-cap.

The mammalian fauna of the QSM and PPM is in several respects 'intermediate' in character, which is in keeping with the environmental changes of the period in question. Although it is essentially 'African' in character, it includes descendants of several Miocene immigrants from Eurasia (e.g. the three-toed horse, *Hipparion*, and the bear, *Agriotherium*). The composition of certain groups (e.g. the hyaenas) still reflected a pattern more characteristic of the Miocene than the Quaternary. However, early representatives of successful Quaternary lineages are recorded (e.g. the white rhinoceros, *Ceratotherium*). While individual taxa represent advances over their Miocene ancestors, many were much less specialized than their Quaternary descendants (e.g. the seal, *Homiphoca capensis*). Some 'tropical' elements were still present (e.g. parrots, giraffes), but the moderating climate might already have caused some to become extinct, or nearly extinct (e.g. crocodiles, primates).

Faunal evidence of age is in good accord with the geological evidence, although absolute, or chronometric, dates for the various elements in the succession are still lacking.

In a little more than a decade the Langebaanweg succession has become one of the more intensively studied and best understood complexes of late Tertiary deposits in southern Africa. It has also become the source of the largest assemblage of late Tertiary vertebrates known anywhere in Africa. The unique set of geological, botanical and faunal data already available have combined to provide an unparalleled insight into the nature of local late Tertiary environments and the changes that they underwent. In spite of all this,

there is still a considerable potential for further research, and the significance of this area in southern African Cenozoic studies should increase still further.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
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e.g. Therocephalia, but therocephalian

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Reference to the author should be expressed in the third person

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'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

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Q. B. HENDEY

PALAEOECOLOGY OF THE LATE
TERTIARY FOSSIL OCCURRENCES IN
'E' QUARRY, LANGEBAANWEG,
SOUTH AFRICA, AND A REINTERPRETATION
OF THEIR GEOLOGICAL CONTEXT

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OF THE SOUTH AFRICAN
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CAPE TOWN



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KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.

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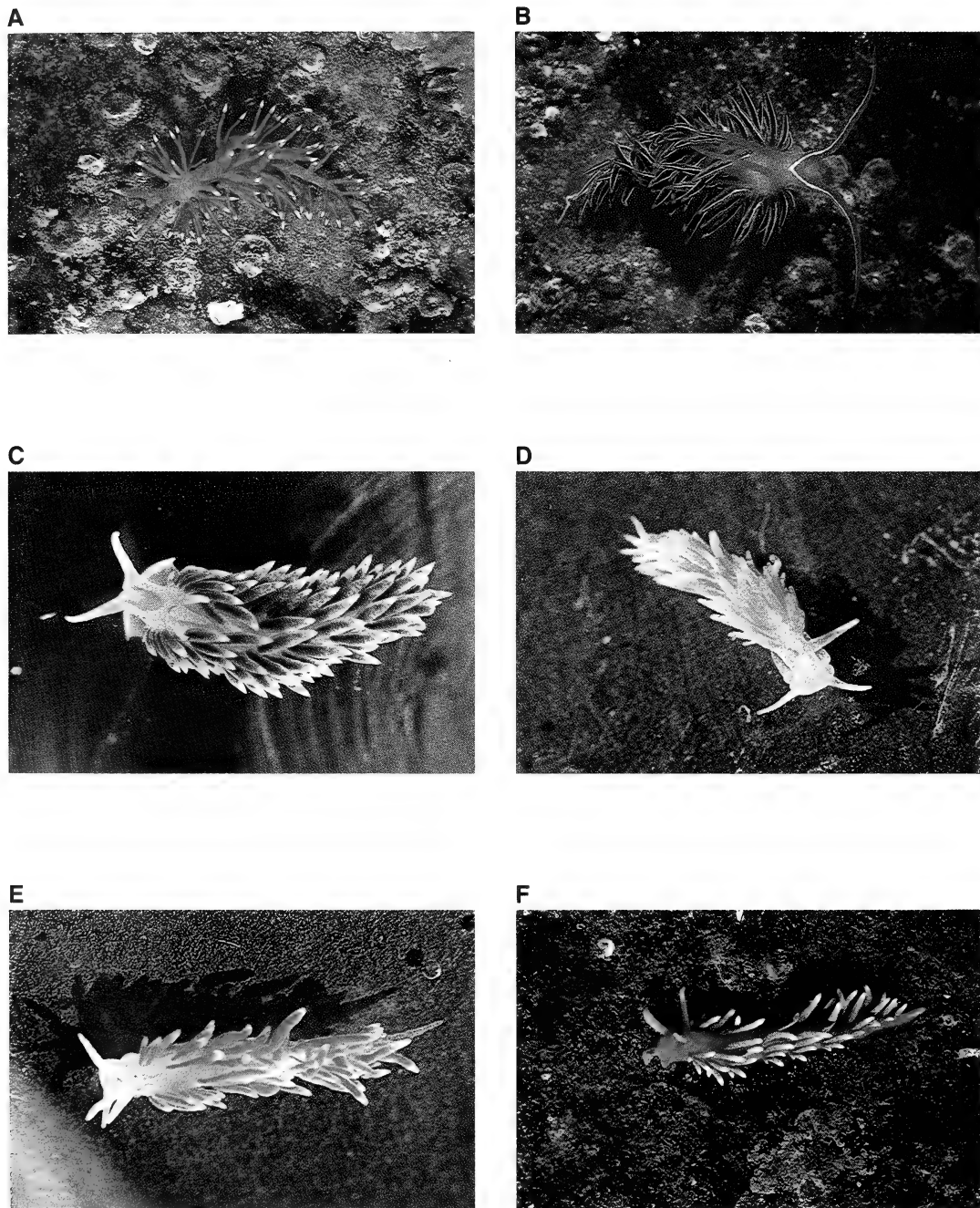


Fig. 1.

A. *Flabellina funeka* sp. nov. B. *Flabellina capensis* (Thiele, 1925). C. *Aeolidiella indica* Bergh, 1888a. D. *Catriona columbiana* (O'Donoghue, 1922). E. *Catriona casha* sp. nov. F. *Cuthona speciosa* (Macn e, 1954) with lilac cerata.

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DESCRIPTION AND REVISION OF SOME
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NUDIBRANCHIA (MOLLUSCA, GASTROPODA)

By

T. M. GOSLINER
&
R. J. GRIFFITHS

Cape Town Kaapstad

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By

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South African Museum

&

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(With 22 figures and 5 tables)

[MS. accepted 2 December 1980]

ABSTRACT

This study examines aeolids of the families Flabellinidae, Aeolidiidae, Tergipedidae, and Embletoniidae from South Africa. The genus *Coryphella* Gray, 1850, is regarded as a junior synonym of *Flabellina* Voigt, 1834. *Flabellina funeka* sp. nov. is described and *Flabellina capensis* (Thiele, 1925) is rediscovered from the Cape Peninsula. *Aeolidiella indica* Bergh, 1888, is designated as the senior synonym of *A. saldanhensis* Barnard, 1927, and *A. multicolor* Macnae, 1954, from South Africa, as well as several other species from other parts of the world. *Catriona columbiana* (O'Donoghue, 1922) is newly recorded from South Africa and *C. casha* sp. nov. is described. *Cuthona speciosa* (Macnae, 1954) is redescribed and transferred to *Cuthona*. *Embletonia gracilis* Risbec, 1928, is recorded from South Africa.

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INTRODUCTION

The aeolidacean nudibranch fauna of South Africa has been sporadically and poorly studied. Bergh (1907) recorded the cosmopolitan, pelagic species, *Glaucus atlanticus* and Thiele (1925) described the external morphology and radula of *Coryphella capensis* based on a single specimen collected off Plettenberg Bay. Barnard (1927) studied the external morphology and radula of

Aeolidiella saldanhensis, *Godiva quadricolor* (as *Hervia*), *Cratena capensis*, and *Facelina faurei*. The only complete descriptions of South African aeolid nudibranchs were provided by Macnae (1954). He further elucidated the morphology of species described by Bergh and Barnard and described seven additional taxa. Of the 13 species of aeolids recorded from South Africa to date, 8 are members of the Facelinidae, 2 of the Aeolidiidae, and 1 each of the Flabellinidae, Tergipedidae, and Glaucidae.

Our collections and morphological study of some South African opisthobranchs have yielded several new taxa, of which two species are here described. Two additional species, not previously recorded from South Africa, are described in detail and the descriptions of three species previously recorded from South Africa are amplified and their systematic placement revised.

Family **Flabellinidae**

Flabellina funeka sp. nov.

Figs 1A, 2–4

Material

Holotype

South African Museum, Cape Town, SAM-A34317, 10 m depth, Castle Rocks, False Bay (34°14'S 18°29'E), 17 January 1980.

Paratypes

SAM-A34318, 10 m depth, Castle Rocks, False Bay (34°14'S 18°29'E), 17 January 1980

SAM-A34319, 10 m depth, Venus Pool, False Bay (34°17'S 18°28'E), 6 January 1980

SAM-A34320, 17 m depth, New Harbour wall, Hermanus (34°17'S 19°15'E), 11 October 1971

SAM-A34321, 17 m depth, New Harbour wall, Hermanus (34°17'S 19°15'E), 11 October 1971

Etymology

'Funeka' is derived from Zulu, meaning to be sought after, owing to its beauty.

External morphology

The fully mature animals (Fig. 1A) are 9 to 40 mm in length, when actively crawling. The oral tentacles are shorter than the rhinophores and are basally thickened (Fig. 2A). The foot corners are short and well developed. When fully extended they are held at an angle of 90° from the foot, but are recurved inwardly when the animal's head is raised. The foot is slender and transversely grooved anteriorly. The rhinophores are conical with 10 to 14 transverse lamellae which may be complete or interrupted (Fig. 2B). The cerata arise from

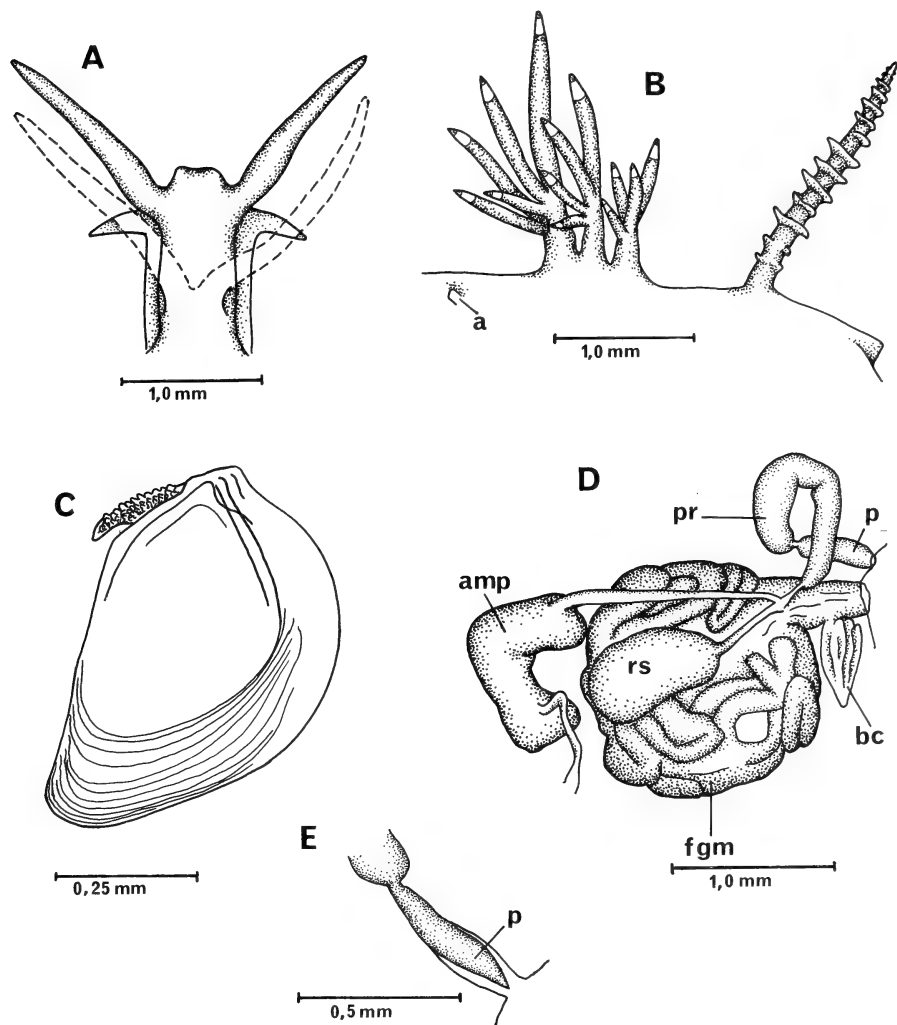


Fig. 2. *Flabellina funeka* sp. nov. A. Dorsal view of head. B. Lateral view of pedunculate cerata and rhinophore. C. Jaw. D. Reproductive system. E. Penis.

compound peduncles which generally contain two or three major subdivisions. The right anterior digestive branch is formed by 2 or 3 compound peduncles with 4 to 6 cerata in the anteriormost cluster, 9 to 10 cerata in the second, and 6 to 10 in the third. In some instances the first and second peduncles are incompletely separated, thus forming a single, larger peduncle. These peduncles are followed by the long interhepatic space. In the posterior digestive branch there are 7 to 9 peduncles per side. They consist of 7 to 11, 6 to 9, 5 to 7, 4 to 6, 2 to 4, 1 to 3, 1 to 2, 1, 1 cerata per peduncle. The pleuroproct anus

is situated in the middle of the interhepatic space. The gonopores are ventral to the first and second peduncles of the right anterior digestive branch.

The body surface is covered by vivid mauve pigment. The rhinophores and oral tentacles are tipped with opaque white pigment. The ceratal peduncles are purple but the ceratal epidermis is translucent. The vermilion-red digestive gland does not entirely fill the lumen of the cerata. Each ceras has a subapical band of opaque white pigment.

Internal morphology

The buccal mass is small relative to the size of the animal. There are well-developed oral glands which extend into the anteriormost ceratal peduncle. The jaws (Fig. 2C) are thin and broadly ovoid with 5 to 6 rows of denticles on the masticatory border. The outer row contains 23 to 33 prominent denticles. The triserial radula (Fig. 3) consists of 30 to 35 rows of teeth. The rachidian teeth are broad with a thick basal portion and 5 to 10 shallow to deeply incised denticles on each side of the slightly larger central cusp. The lateral teeth are triangular, basally arched and terminate in an acute apex. The number of denticles on the inner face of the laterals is variable. In some instances denticles may be absent, but there are commonly 7 to 12.

The reproductive system (Fig. 2D) has a large, slightly convoluted ampulla. A postampullary duct of variable length gives rise to the duct of the receptaculum seminis. The large, pear-shaped receptaculum seminis lies ventral

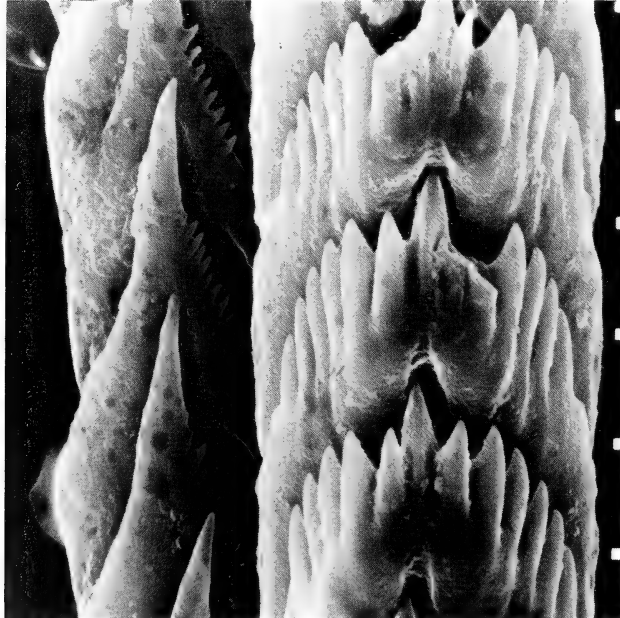


Fig. 3. *Flabellina funeka* sp. nov. Scanning electron micrograph of the radula. Scale: 10 μ m between squares.

to the ampulla. Slightly more distally from the receptaculum duct, the postampullary duct bifurcates into a short oviduct and a longer vas deferens. The thick, prostatic vas deferens constricts sharply and terminates in a short, conical, unarmed penial papilla (Fig. 2E). The female gland mass is well developed with the mucous gland forming the largest portion. The saccate bursa copulatrix is situated near the female gonopore and appears to have a glandular epidermis.

Natural history

Flabellina funeka has been found at several localities in False Bay and at Hermanus. It has only been found subtidally in 7 to 17 m of water. It appears to feed exclusively on members of the gymnoblastic hydroid genus, *Eudendrium*.

Egg mass

The egg mass of *Flabellina funeka* (Fig. 4) is highly convolute and undulate, consisting of several whorls. There is a single egg per capsule.

Discussion

The generic distinction between *Coryphella* Gray, 1850, and *Flabellina* Voigt, 1834, is based upon the manner in which the cerata are inserted into the notum. *Coryphella* is characterized by cerata that insert directly into the notum, while a stalk or peduncle of notal tissue is found in species of *Flabellina*. While the majority of species can be separated using this feature, several others are more problematic. *Coryphella iodinea* (Cooper, 1862) (MacFarland 1966), *C. pellucida* (Alder & Hancock, 1843) (Kuzirian 1979), *C. cynara* Marcus & Marcus, 1967, *C. pricei* MacFarland, 1966, and *C. trilineata* O'Donoghue, 1921 (MacFarland 1966, as *C. fisheri*) possess cerata on cushions that are somewhat more elevated than in most species of *Coryphella*, but less pronounced than those of *Flabellina*. This fact led MacFarland (1966) to erect the genus

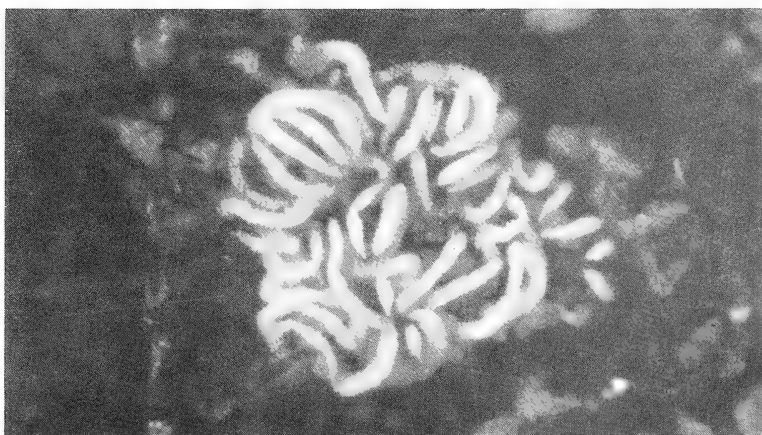


Fig. 4. *Flabellina funeka* sp. nov. Egg mass at $5 \times$ magnification.

Flabellinopsis for *Aeolis iodinea* Cooper, 1862. Marcus and Marcus (1967) quite correctly noted that this further complicates the problem of separating *Flabellina* and *Coryphella* and suggested that *Flabellinopsis* be regarded as a junior synonym of *Coryphella*.

If one compares the type species of *Coryphella* (*Eolis rufibranchialis* Johnston, 1832 = *Eolidia verrucosa* M. Sars, 1829) with that of *Flabellina* (*Doris affinis* Gmelin, 1791), several other differences appear. In *Coryphella verrucosa* the pleuroproctic anus is situated near the anterior limit of the right posterior digestive branch (Kuzirian 1979) while in *Flabellina affinis* it is situated in the interhepatic space. In *Coryphella verrucosa* the rhinophores are slightly rugose (Kuzirian 1979) while in *Flabellina affinis* they possess 25 to 28 annulations (Bergh 1875). These and other morphological criteria of *Coryphella verrucosa*, *Flabellina affinis* and species which appear to be intermediate between *Coryphella* and *Flabellina* are compared in Table 1. Other species of *Flabellina* were considered by Gosliner (1980). Analysis of the features listed in Table 1 demonstrates several morphological trends. Within the Flabellinidae there is a tendency for the cerata to become modified into more discrete clusters and for these clusters to become elevated from the notum on peduncles. The rhinophores can be smooth, rugose, annulate or perfoliate and this appears to be a morphological sequence to increase sensory surface area. All species of *Flabellina* possess perfoliate rhinophores except for *F. affinis*, which has annulate rhinophores. There is also a tendency towards the anterior migration of the anus into the interhepatic space. Despite these major trends within the family, it is difficult to find a high degree of correlation of these characters among species that are intermediate between *Coryphella* and *Flabellina*. Of species with somewhat pedunculate cerata, *C. pellucida* retains smooth rhinophores, *C. pedata* has rugose rhinophores, *C. pricei* and *C. trilineata* have annulate rhinophores, and *C. cynara* and *C. iodinea* have perfoliate ones. In *C. iodinea* and *C. trilineata* the anus is found posteriorly while in *C. cynara*, *C. pedata*, *C. pellucida*, and *C. pricei* it is in the interhepatic space. Radular and reproductive characters provide no additional basis on which to separate the genera.

Mayr (1969) suggested that a distinct morphological gap should exist between genera. The presence of intermediate forms with poor correlation of morphological characteristics suggests that maintenance of the generic separation of *Coryphella* and *Flabellina* is untenable. We therefore regard *Coryphella* Gray, 1850, as a junior subjective synonym of *Flabellina* Voigt, 1834, syn. nov. on the basis of priority. The species regarded as members of *Flabellina* are as follows:

Flabellina affinis (Gmelin, 1791)

Doris affinis Gmelin, 1791

Flabellina affinis (Gmelin, 1791), Voigt, 1834

Flabellina albomarginata (Miller, 1971)

Coryphella albomarginata Miller, 1971

Flabellina albomarginata (Miller, 1971)—comb. nov.

Flabellina alisonae Gosliner, 1980

- Flabellina annuligera* (Bergh, 1900)
Samla annuligera Bergh, 1900
Flabellina annuligera (Bergh, 1900), Miller, 1971
Flabellina athodona (Bergh, 1875)
Coryphella athodona Bergh, 1875
Flabellina athodona (Bergh, 1875)—comb. nov.
Flabellina barentsi (Vayssière, 1913)
Coryphella barentsi Vayssière, 1913
Flabellina barentsi (Vayssière, 1913)—comb. nov.
Flabellina babai Schmekel, 1970
Flabellina berghi (Vayssière, 1888)
Coryphella berghi Vayssière, 1888
Flabellina berghi (Vayssière, 1888)—comb. nov.
Flabellina browni (Picton, 1980)
Coryphella browni Picton, 1980
Flabellina browni (Picton, 1980)—comb. nov.
Flabellina borealis (Odhner, 1922)
Coryphella borealis Odhner, 1922
Flabellina borealis (Odhner, 1922)—comb. nov.
Flabellina californica (Bergh, 1904)
Coryphella californica Bergh, 1904
Flabellina californica (Bergh, 1904)—comb. nov.
Flabellina capensis (Thiele, 1925)
Coryphella capensis Thiele, 1925
Flabellina capensis (Thiele, 1925)—comb. nov.
Flabellina cooperi (Cockerell, 1901)
Coryphella cooperi Cockerell, 1901
Flabellina cooperi (Cockerell, 1901)—comb. nov.
Flabellina cynara (Marcus & Marcus, 1967)
Coryphella cynara Marcus & Marcus, 1967
Flabellina cynara (Marcus & Marcus, 1967)—comb. nov.
Flabellina dushia (Marcus & Marcus, 1963)
Coryphella dushia Marcus & Marcus, 1963
Flabellina dushia (Marcus & Marcus, 1963)—comb. nov.
Flabellina engeli Marcus & Marcus, 1968
Flabellina falklandica (Eliot, 1907)
Coryphella falklandica Eliot, 1907
Flabellina falklandica (Eliot, 1907)—comb. nov.
Flabellina frigida (Grieg, 1905)
Coryphella frigida Grieg, 1905
Flabellina frigida (Grieg, 1905)—comb. nov.
Flabellina fusca (O'Donoghue, 1921)
Coryphella fusca O'Donoghue, 1921
Flabellina fusca (O'Donoghue, 1921)—comb. nov.
Flabellina gracilis (Alder & Hancock, 1844)
Eolis gracilis Alder & Hancock, 1844
Coryphella gracilis (Alder & Hancock, 1844), Alder & Hancock, 1855
Flabellina gracilis (Alder & Hancock, 1844)—comb. nov.
Flabellina incognita (Derjugin, 1926)
Coryphella barentsi Derjugin, 1924, *non* Vayssière, 1913
Coryphella stimpsoni incognita Derjugin, 1926, *non* Verrill, 1879
Flabellina incognita (Derjugin, 1926)—comb. nov.
Flabellina iodinea (Cooper, 1862)
Aeolis (Phidiana?) iodinea Cooper, 1862
Flabellinopsis iodinea (Cooper, 1862), MacFarland, 1966
Coryphella iodinea (Cooper, 1862), Marcus & Marcus, 1967
Flabellina iodinea (Cooper, 1862)—comb. nov.

TABLE 1

Comparison of some species of *Coryphella* and *Flabellina*.

	Distribution	Coloration	Cerata	Rhinophores	Radular rows	Denticles per side of rachidian
<i>Flabellina affinis</i>	Mediterranean	body and cerata violet; speckled, pale brown	on compound peduncles	18-25 annulations	34	6-7
<i>Coryphella verrucosa</i>	North Atlantic Circumboreal	body transparent white; cerata red (rarely green) white tips	not elevated	rugose	13-20	4-8
<i>Flabellina funeka</i>	South Africa	body mauve; cerata red, white tips	on compound peduncles	10-14 annulations	30-35	5-8
<i>Coryphella cynara</i>	Gulf of California	body semi-transparent blue; cerata orange-brown, white tips, body with blue lines	on simple 'cushions'	30 perfoliations	16	7-9
<i>Coryphella fusca</i>	North Pacific	body transparent, cerata deep brown, opaque tips	not elevated	32-38 annulations	19	4-7
<i>Coryphella iodinea</i>	North-eastern Pacific	body purple; cerata orange	markedly elevated	46-80 perfoliations	22	14-16
<i>Coryphella pedata</i>	European Atlantic Mediterranean	body violet; cerata orange-red, white tips	slight elevation	rugose	20	3-6
<i>Coryphella pellucida</i>	North Atlantic	body transparent, white; cerata carmine, white tips	markedly elevated	smooth	30-40	8-11
<i>Coryphella pricei</i>	California	body translucent white, cerata red-orange or olive green	slight elevation	c. 20 annulations	19	6-8
<i>Coryphella trilineata</i>	North-eastern Pacific	body translucent grey, cerata orange-red	first group only slightly elevated	14-20 annulations	17-18	5-8

Flabellina islandica (Odhner, 1937)*Coryphella islandica* Odhner, 1937*Paracoryphella islandica* (Odhner, 1937), Miller, 1971*Flabellina islandica* (Odhner, 1937)—comb. nov.*Flabellina japonica* (Volodchenko, 1941)*Coryphella japonica* Volodchenko, 1941*Flabellina japonica* (Volodchenko, 1941)—comb. nov.*Flabellina lineata* (Lovén, 1846)*Aeolis lineata* Lovén, 1846*Aeolis argentolineata* Costa, 1866, Trinchese, 1877*Coryphella lineata* (Lovén, 1846), Bergh, 1875*Flabellina lineata* (Lovén, 1846)—comb. nov.*Flabellina longicaudata* (O'Donoghue, 1922)*Coryphella longicaudata* O'Donoghue, 1922*Flabellina longicaudata* (O'Donoghue, 1922)—comb. nov.*Flabellina macassarana* Bergh, 1905*Flabellina nobilis* (Verrill, 1880)*Coryphella nobilis* Verrill, 1880*Flabellina nobilis* (Verrill, 1880)—comb. nov.*Flabellina orientalis* (Volodchenko, 1941)*Coryphella orientalis* Volodchenko, 1941*Flabellina orientalis* (Volodchenko, 1941)—comb. nov.

Denticles on laterals	Position of receptaculum seminis	Position of bursa copulatrix	Penis	Anal position	Foot corners	Reference
6	distal or rarely proximal	distal	elongate, conical	interhepatic space	short, stout	Bergh 1875; Vayssière 1913; Schmekel 1970
7-12	proximal	distal	trumpet-shaped	lateral on anterior margin of second hepatic group	moderate length	Thompson & Brown 1976; Kuzirian 1979
0-12	proximal	distal	short, conical	interhepatic space	short, stout	present study
12-15	absent	distal	bulbous, papillate	interhepatic space	long, slender	Marcus & Marcus 1967
3-5	unknown	unknown	unknown	unknown	long, slender	O'Donoghue 1921
11-16	absent	distal	short, conical	lateral, below margin of second hepatic group	short, stout	MacFarland 1966; Marcus & Marcus 1967
5-7	two proximal	absent	bulbous	interhepatic space	short, stout	Alder & Hancock 1848, Thompson & Brown 1976, Schmekel 1970
smooth	proximal	distal	unknown	interhepatic space	long, slender	Kuzirian 1979
smooth	absent	distal	short, conical	interhepatic on anterior lateral edge of second group	stout, tapering	MacFarland 1966
6-12	proximal	distal	short, conical, tip pointed and curved	lateral on anterior margin of second hepatic group	short, pointed	O'Donoghue 1921 MacFarland 1966

Flabellina ornata (Risbec, 1928)

Coryphella ornata Risbec, 1928

Flabellina ornata (Risbec, 1928), Baba, 1955

Flabellina parva (Hadfield, 1963)

Coryphella parva Hadfield, 1963

Flabellina parva (Hadfield, 1963)—comb. nov.

Flabellina pedata (Montagu, 1815)

Doris pedata Montagu, 1815

Eolis landsburgii Alder & Hancock, 1846, Alder & Hancock, 1855

Coryphella pedata (Montagu, 1815), Odhner, 1939

Flabellina pedata (Montagu, 1815)—comb. nov.

Flabellina pellucida (Alder & Hancock, 1843)

Eolis pellucida Alder & Hancock, 1843

Coryphella pellucida (Alder & Hancock, 1843), Gray, 1850

Flabellina pellucida (Alder & Hancock, 1843)—comb. nov.

Flabellina poenicia (Burn, 1957)

Hervia? poenicia Burn, 1957

Coryphella poenicia (Burn, 1957), Burn, 1962

Flabellina poenicia (Burn, 1957)—comb. nov.

Flabellina polaris (Volodchenko, 1946)

Coryphella polaris Volodchenko, 1946

Flabellina polaris (Volodchenko, 1946)—comb. nov.

- Flabellina pricei* (MacFarland, 1966)
Coryphella pricei MacFarland, 1966
Flabellina pricei (MacFarland, 1966)—comb. nov.
- Flabellina robusta* (Trinchese, 1874)
Coryphella robusta Trinchese, 1874
Flabellina robusta (Trinchese, 1874)—comb. nov.
- Flabellina rubrolineata* (O'Donoghue, 1929)
Coryphellina rubrolineata O'Donoghue, 1929
Coryphella rubrolineata (O'Donoghue, 1929), Miller, 1971
Flabellina rubrolineata (O'Donoghue, 1929)—comb. nov.
- Flabellina salmonacea* (Couthouy, 1838)
Eolis salmonacea Couthouy, 1838
Coryphella salmonacea (Couthouy, 1838), Bergh, 1864
Flabellina salmonacea (Couthouy, 1838)—comb. nov.
- Flabellina stohleri* Bertsch & Ferreira, 1974
- Flabellina telja* Marcus & Marcus, 1967
- Flabellina trilineata* (O'Donoghue, 1921)
Coryphella trilineata O'Donoghue, 1921
Flabellina trilineata (O'Donoghue, 1921)—comb. nov.
- Flabellina trophina* (Bergh, 1894)
Himatella trophina Bergh, 1894
Himatina trophina (Bergh, 1894), Thiele, 1931
Coryphella trophina (Bergh, 1894), Marcus, 1961a
Flabellina trophina (Bergh, 1894)—comb. nov.
- Flabellina verrucosa* (M. Sars, 1829)
Eolidia verrucosa M. Sars, 1829
Eolis rufibranchialis Johnston, 1832, Odhner, 1939
Coryphella verrucosa (M. Sars, 1829), Gray, 1850
Flabellina verrucosa (M. Sars, 1829)—comb. nov.
- Flabellina verta* (Marcus, 1970)
Coryphella verta Marcus, 1970
Flabellina verta (Marcus, 1970)—comb. nov.
- Flabellina violacea* (Risbec, 1928)
Coryphella ornata violacea Risbec, 1928
Coryphella violacea Risbec, 1928, Gosliner, 1980
Flabellina violacea (Risbec, 1928)—comb. nov.

Several species of *Flabellina* possess purple ground colour: *Flabellina affinis* (Gmelin, 1791), *F. pedata* (Montagu, 1815), *F. iodinea* (Cooper, 1862), *F. annuligera* (Bergh, 1900), *F. violacea* (Risbec, 1928), *F. telja*, Marcus & Marcus, 1967, *F. babai* Schmekel, 1970, and *F. alisonae*, Gosliner, 1980. *Flabellina affinis*, *F. annuligera*, *F. telja*, *F. babai*, and *F. alisonae* have distinctly pedunculate cerata; however, the peduncles are simple except in *F. affinis*. Of the described species of *Flabellina*, *F. affinis* is most similar to *F. funeka* but differs in several significant features. The cerata of *F. affinis* are purple, while in *F. funeka* they are red. There are 25 to 28 annulae on the rhinophores of *F. affinis*, while there are 10 to 14 in *F. funeka*. *F. affinis* possesses a single compound ceratal peduncle in the right anterior digestive branch, while *F. funeka* has 2 or 3 compound branches. There are no significant radular differences between the two species. The reproductive systems of *F. affinis* and *F. funeka* differ in two important features. In *F. affinis* the prostate is thin and highly convoluted (Schmekel 1970) while in *F. funeka* it is

thick and significantly shorter. In *F. affinis* the penial papilla is slender and elongate, while it is short and conical in *F. funeka*. Schmekel (1970) described a typical and an atypical form of the reproductive system of *F. affinis*. In the typical form the receptaculum seminis and bursa copulatrix are both distal to the female gland mass, while in the atypical form the receptaculum is proximally situated. The latter configuration is found in *F. funeka*. These differences between *F. funeka* and *F. affinis* are consistent and warrant specific separation.

Flabellina capensis (Thiele, 1925)

Figs 1B, 5–6

Coryphella capensis Thiele, 1925: 287, pl. 34 (fig. 1).

Flabellina capensis (Thiele, 1925) **comb. nov.**

Material

University of Cape Town, Department of Zoology

CP 811, 10 m depth, Oatlands Point, False Bay (34°12'S 18°27'E), 10 December 1972, 2 specimens

CP 819, 10 m depth, Castle Rocks, False Bay (34°14'S 18°29'E), 13 May 1973, 1 specimen

CP 827, 10 m depth, Oudekraal, west coast Cape Peninsula (33°59'S 18°21'E), 20 February 1974, 1 specimen

CPR 86C, 17 m depth, New Harbour wall, Hermanus (34°27'S 19°15'E), 11 October 1974, 1 specimen

South African Museum, Cape Town

SAM-A34878, 18 m depth, Castle Rocks, False Bay (34°14'S 18°29'E), 17 January 1980, 1 specimen

SAM-A34879, 10 m depth, Castle Rocks, False Bay (34°14'S 18°29'E), 30 March 1980, 4 specimens

SAM-A34880, 10 m depth, Rooi Els, Cape Hangklip (34°18'S 18°49'E), 23 January 1980, 1 specimen

SAM-A34881, 10 m depth, Castle Rocks, False Bay (34°14'S 18°29'E), 11 February 1980, 1 specimen

Distribution

Cape Province, Cape Peninsula to Plettenberg Bay.

External morphology

Live animals (Fig. 1B) may reach 43 mm in length; they are extremely active and bristle their cerata when disturbed. The body is long and slender. The oral tentacles are long and tapered, attaining 12 mm in length in a 26 mm animal. The shorter rhinophores are rugose and nodular (Fig. 5A). The foot is transversely grooved anteriorly with acute tentacular foot corners. The cerata

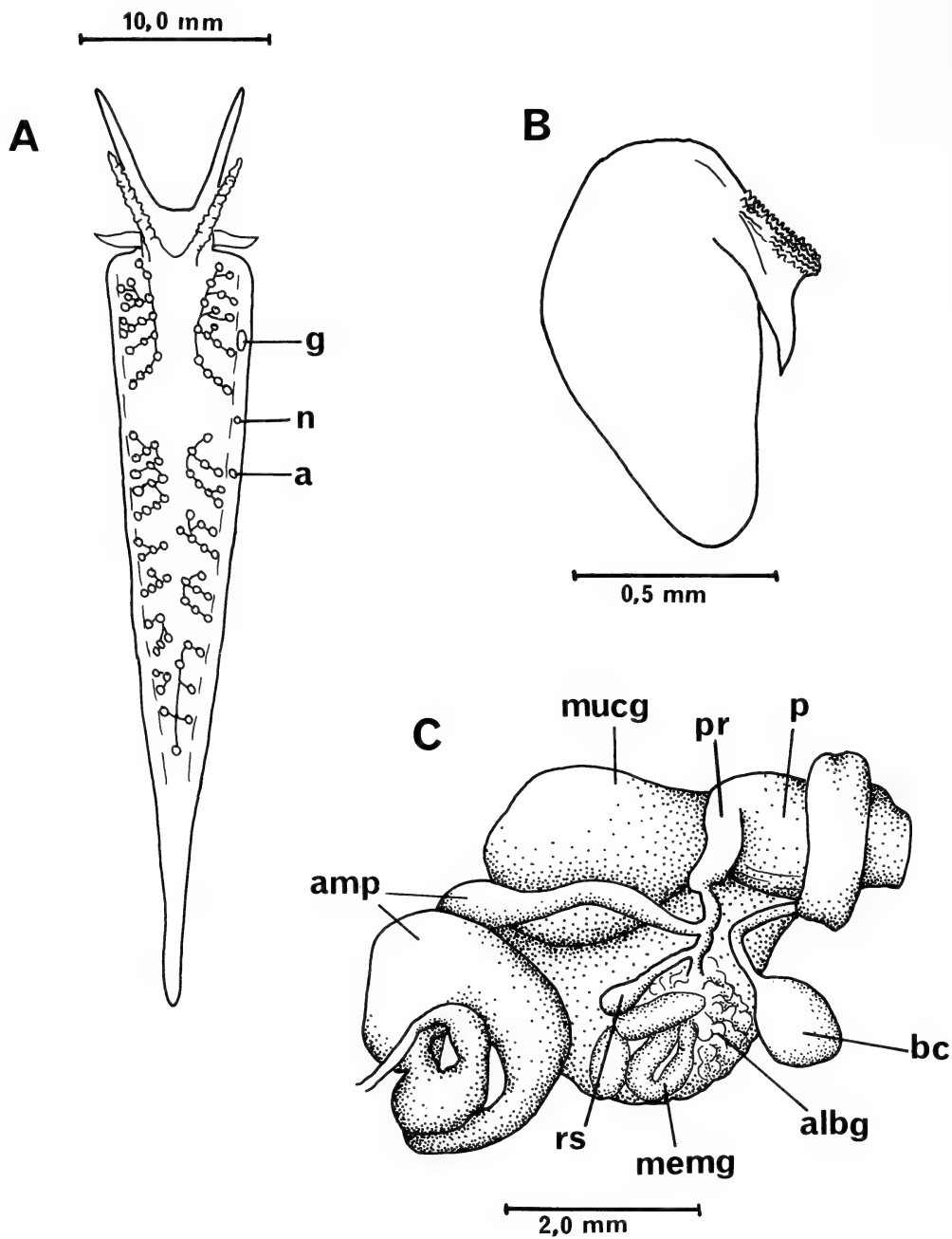


Fig. 5. *Flabellina capensis* (Thiele, 1925). A. Dorsal view of animal showing branching of the digestive system and position of the gonopores, nephroproct and anus.

B. Jaw. C. Reproductive system.

are arranged in linear rows that are not clearly separated into distinct clusters (Fig. 5A). There are up to 8 ceratal rows in the right anterior digestive system, followed by as many as 17 rows per side in the posterior digestive branches. The pleuroproct anus is ventral to the second or third ceratal row of the posterior digestive system and the nephroproct is in the interhepatic space anterior to the anus. The gonopore is ventral to the third and fourth ceratal rows of the right anterior digestive branch.

The animals are translucent white with red or brown ceratal cores. Opaque white markings are distributed as follows: two lines, one on the dorsal surface of each cephalic tentacle, which converge and terminate on the head immediately anterior to the rhinophores; an anterior and posterior vertical line and varied spots on each ceras; and a line on the dorsal surface of the posterior 3 to 5 mm of the foot.

Internal morphology

The jaws (Fig. 5B) are delicate and elongate with 5 to 6 rows of irregularly shaped denticles on the masticatory border. The triseriate radula (Fig. 6) contains 13 to 15 rows of teeth. The rachidian teeth are sharply arched with 6 to 8 acute denticles on each side of the slightly more prominent central cusp. The lateral teeth are triangular with a thickened basal portion. The inner margin of



Fig. 6. *Flabellina capensis* (Thiele, 1925). Scanning electron micrograph of the radula. Scale: 30 μ m between squares.

each lateral tooth bears 10 to 13 denticles. There are no obvious labial glands around the buccal mass.

The reproductive system (Fig. 5C) consists of a large, slightly convoluted ampulla that joins the elongate receptaculum seminis via a short duct. The vas deferens is short, with a small prostatic portion that expands into a hollow paddle-shaped penis. At the distal end of the female gland mass a bursa copulatrix lies ventral to the receptaculum seminis and enters the female atrium. The bursa may be elongate or spherical in shape.

Natural history

Flabellina capensis feeds on the gymnoblastic hydroid *Eudendrium* sp. in shallow subtidal waters.

Discussion

Flabellina capensis was described by Thiele (1925) from a single specimen collected off Plettenberg Bay, South Africa. He stated that the preserved animal was 10 mm long with elongate oral tentacles and nodular rhinophores. The triseriate radula consisted of 17 rows of teeth. The rachidian teeth were arched with 8 to 9 denticles on each side of the slightly prominent central cusp. The triangular laterals had 9 to 12 denticles on their inner face. Although the species was poorly described, the external features bear a strong resemblance to the present material. The radular teeth of our specimens and those described by Thiele (1925, pl. 66 (fig. 1)) are very similar in shape and number of denticles on the rachidian and lateral teeth. The material in this study is consistent with these characteristics and is considered to be conspecific with *Flabellina capensis*.

Flabellina capensis resembles the European *Flabellina lineata* (Lovén, 1846) in its external and internal morphology. Both species possess elongate oral tentacles, reddish colour with numerous white lines (Thompson 1976; Thompson & Brown 1976) and radular teeth which are similar in form (Odhner 1939). The reproductive systems are virtually identical (Schmekel 1970). There are, however, consistent differences in the external morphology. The South African material possesses opaque white lines along the oral tentacles which converge and terminate just anterior to the rhinophores, while in *F. lineata* a white line extends along the dorsomedial surface for the entire length of the animal. There are also two lateral lines along the body in *F. lineata*. Odhner (1939) and Thompson & Brown (1976) described the presence or absence of opaque white lines on the notum in *F. lineata*. *F. lineata* also has white lines on the posterior surface of the rhinophores, which are absent in specimens of *F. capensis*. While both species have the opaque white line on the anterior face of each ceras, there is an additional line on the posterior face of the cerata in *F. capensis*. The rhinophores are largely smooth in *F. lineata*, while they are strongly wrinkled to nodular in *F. capensis*. Despite their similarity, *F. capensis* and *F. lineata* appear to have several consistent differences which are here considered sufficient to warrant specific separation. Picton (1980) has similarly suggested separation of *F. lineata* and *F. browni* which occur sympatrically in the British Isles.

Family **Aeolidiidae***Aeolidiella indica* Bergh, 1888

Figs 1C, 7–10

- Aeolidiella indica* Bergh, 1888a: 755, pl. 78 (figs 1–2).
Aeolidiella orientalis Bergh, 1888b: 673, pl. 16 (figs 8–13) **syn. nov.**
Aeolidiella saldanhensis Barnard, 1927: 201, figs 2–3 **syn. nov.**
Aeolidiella hulli Risbec, 1928: 262, fig. 88, pl. 10 (fig. 7), pl. 12 (fig. 4) **syn. nov.**
Aeolidiella takanosimensis Baba, 1930: 122, fig. 4a–b, pl. 4 (fig. 5a–c) **syn. nov.**
Aeolidiella multicolor Macnae, 1954: 36, figs 27–29, pl. 2 (fig. 4) **syn. nov.**
Aeolidiella lurana Marcus & Marcus, 1967: 115, figs 149–150 **syn. nov.**

Material

University of Cape Town, Department of Zoology

LB 572A, intertidal Schaapen Island, Saldanha Bay (33°06'S 18°02'E), 6 May 1973

CP 797, intertidal, Clovelly, False Bay (34°05'S 18°26'E), 16 April 1972

Other material

intertidal, Langebaan Lagoon (33°06'S 18°02'E), 5 December 1979

intertidal, Onrus (34°26'S 19°10'E), 5 February 1980

intertidal, Knysna Lagoon (34°05'S 23°04'E), 3 March 1980

intertidal, Langebaan Lagoon (33°06'S 18°02'E), 6 April 1980

intertidal, Coffee Bay, Transkei (31°59'S 29°09'E), 7 March 1981*

Distribution

Japan (Baba 1930, 1949, 1979); California (Sphon 1971); Mexico (Ferreira & Bertsch 1975); Hawaii (Gosliner 1980); Mauritius (Bergh 1888a); Noordwachter Island (Bergh 1888b); Red Sea (Eliot 1908); Tanzania (Edmunds 1969); New Caledonia (Risbec 1928); Naples (Schmekel 1970); Brazil (Marcus & Marcus 1967).

External morphology

Live mature animals may attain a length of up to 35 mm (Fig. 1C). The conical oral tentacles are slightly longer than the smooth rhinophores. A pair of black eyes are visible at the posterior base of the rhinophores. The foot is transversely grooved anteriorly and rounded, with stout, slightly produced corners. The anterior digestive group contains 7 obliquely set ceratal rows per side, followed by up to 20 rows in the posterior branches (Fig. 7A). The gonopore is situated on the ventral edge of the third to fifth rows of the right anterior digestive group and the cleioproctic anus between the third and fourth rows of the first ceratal group of the right posterior digestive branch.

* Additional data received while in press.

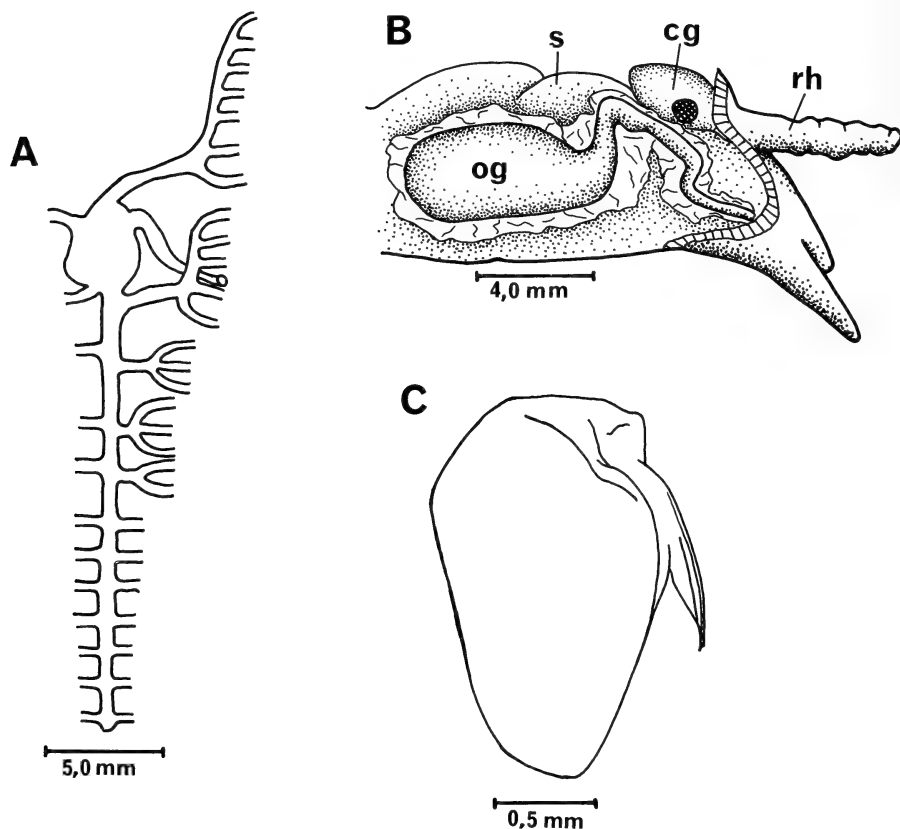


Fig. 7. *Aeolidiella indica* Bergh, 1888a. A. Branching of the digestive system. B. Lateral view showing oral gland. C. Jaw.

The body is translucent white with or without opaque white on the tips of the oral tentacles and rhinophores. The head bears a U-shaped pattern of orange extending from the rhinophores to the base of the oral tentacles. In some specimens, up to half of the base of the U may be filled with orange pigment. Extending posteriorly from the base of the rhinophores are translucent or opaque white areas outlined with orange pigment in the shape of an elongate diamond, followed by a large orange circle outlining the pericardial region. Combination of these two areas of pigmentation has been characterized as a 'Greek vase' by Eliot (1908) in describing *Aeolidiella orientalis*. Posterior to this, a second but smaller circle of orange pigment may occur. Outside of these designs on the dorsum, the back may be covered with orange pigment of varying intensity. The ceratal epithelium is diffusely covered with orange pigment which may be either interrupted by a subapical band of translucent white or overlain with opaque white or pale blue flecks. The digestive gland in the cerata is brown and terminates in a white cnidosac.

Internal morphology

The jaws (Fig. 7C) are broad and ovoid with an elongate, smooth masticatory border. The radula (Fig. 8) bears 15 to 22 teeth that have a widely emarginate anterior margin with a prominent central cusp and 17 to 32 evenly graded lateral denticles on each side. A large oral gland (Fig. 7B) extends on either side of the buccal mass to the posterior end of the stomach. The reproductive system is identical to that described by Macnae (1954, as *Aeolidiella multicolor*).

Natural history

In this study *Aeolidiella indica* was found in the intertidal zone from Langebaan Lagoon, Saldanha Bay to Coffee Bay, Transkei. In all cases it has been found associated with the sea anemone *Anthothoe stimpsonii* (Verrill) upon which it feeds voraciously. In the field, *A. indica* are frequently found aggregated under stones and in the vicinity of their egg masses (Fig. 9).

Discussion

The generic distinctions between *Aeolidiella* Bergh, 1867, and *Spurilla* Bergh, 1864, have been the subject of considerable controversy (Marcus 1961a; Burn 1969; Edmunds 1969). Marcus (1961a) differentiated the taxa on the basis of smooth rhinophores in *Aeolidiella* in contrast to perfoliate rhinophores in *Spurilla*. Burn (1969) noted that several species have rhinophores with bulbous swellings or oblique ribs and stated that the ornamentation of the rhinophores and denticulation of the jaws were not important in the separation of the genera. He suggested that the branching of the 'liver' (digestive gland) and the anal position should serve as more significant criteria for generic separation. However, Burn (1969) included species with both an arch or several rows in the right anterior digestive branch within the genus *Spurilla* (Table 2), and did not specify the anal position for the majority of species he included in this genus. Burn noted that the presence of an anterior accessory digestive branch within the head is unique to *Spurilla*, although its presence has been noted in only three of the seven species which he included in the genus. The final criterion that he used to separate the genera was the presence of broadly emarginate, concave teeth in *Aeolidiella* as opposed to evenly curved teeth in *Spurilla*. However, the radular teeth of the type species, *Aeolidiella soemmerringi* (Leuckart, 1828) Bergh 1867, *non* Leuckart = *A. alderi* (Cocks, 1852) (G. Brown, University of Bristol, 1980 pers. comm.), as well as *A. glauca* (Alder & Hancock, 1845) and *A. sanguinea* (Norman, 1877) are of the same shape as those found in *Spurilla macleayi* (Burn 1969), *S. japonica* (Baba 1949), *S. chromosoma* (Marcus 1961a), *S. olivae* (MacFarland 1966) and *S. alba* (Edmunds 1969). The radular teeth of *Spurilla neapolitana* (Marcus 1955; Gosliner 1980) and *S. orientalis* (Bergh 1905) are evenly curved without emargination of the anterior border. As greater variation occurs among species of *Spurilla* than between *Spurilla* and *Aeolidiella*, the shape of the teeth cannot be utilized for generic separation.

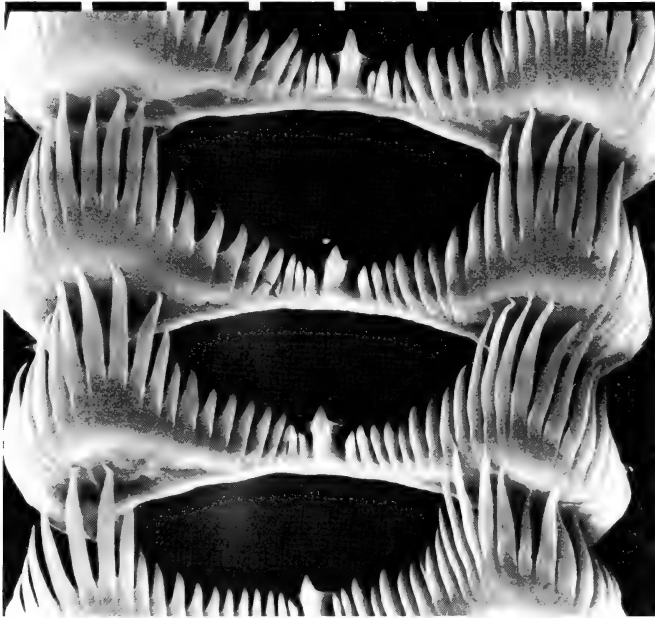


Fig. 8. *Aeolidiella indica* Bergh, 1888a. Scanning electron micrograph of the radula. Scale: 30 μ m between squares.



Fig. 9. *Aeolidiella indica* Bergh, 1888a.
Egg mass at 10 \times magnification.

TABLE 2
Comparison of morphological features of *Spurilla* species.

Species	Distribution of cerata		Rhinophores	Teeth	Anal position	Accessory digestive branch	Reference
	anterior branch	posterior branch					
<i>S. neapolitana</i>	1 arch	1 arch	perfoliate	convex anterior margin, denticles uniformly graded, central denticle reduced in size	within arch of first posterior digestive branch	present	MacFarland 1909; Burn 1969
<i>S. macleayi</i>	1 arch	1 arch	ribbed	emarginate, graded lateral denticles, central same size as lateral denticles	within arch of first posterior digestive branch	unknown	Burn 1969
<i>S. olivae</i>	? 3 or 5 rows	rows	perfoliate	emarginate, denticles evenly graded	? between row 5 and 6	unknown	MacFarland 1966
<i>S. chromosoma</i>	5 to 6 rows	1 arch	perfoliate	emarginate, evenly graded denticles	within arch of first posterior digestive branch	unknown	Marcus 1961a
<i>S. orientalis</i>	3 rows	unknown	? perfoliate	anterior margin convex, uniformly graded denticles	unknown	unknown	Bergh 1905
<i>S. alba</i>	3 or 4	6 rows	knobbed	emarginate, central denticle twice size of laterals	between first and second rows of posterior digestive branch	present	Edmunds 1969; Burn 1969
<i>S. japonica</i>	4 rows	? rows	knobbed	emarginate, central denticle twice size of laterals	middle of first posterior digestive branch	present	Baba 1949

Edmunds (1969), referring to Burn's (1969) discussion, stated that the anus is situated more anteriorly in *Spurilla*. However, in *Spurilla japonica* the anus is situated in the middle of the first ceratal group of the posterior digestive branch (Baba 1949) as is the case in most species of *Aeolidiella*. There are thus inherent problems in separating the genera. If all species of *Spurilla* do, indeed, possess a branch of the anterior digestive system within the head as suggested by Burn (1969), this will serve as an important generic distinction, particularly as it can be found in species with ornamented rhinophores. This character, however, needs to be verified in *S. macleayi*, *S. chromosoma*, *S. olivae*, and *S. orientalis*. If these species do not possess cephalic extensions of the digestive gland, a further possible generic distinction may exist in the structure of the digestive system. In the type species of *Spurilla*, *S. neapolitana*, the right anterior digestive gland consists of a single arch as in *S. macleayi*. However, the remaining species considered as *Spurilla* by Burn (1969) have a series of ceratal rows in the anterior digestive branch, as do all species considered to be members of *Aeolidiella* in this study. This means of separating the genera was followed by Baba (1979). Generic separation of the related aeolid genera *Berghia* and *Baeolidia* is also based on the configuration of the right anterior digestive branch (Gosliner 1980) as is the separation of the facelinid and favorinid aeolids (Miller 1974; Gosliner 1980). Pending additional morphological data with regard to accessory branching of the anterior digestive branch into the head, we prefer to maintain the separation of *Aeolidiella* and *Spurilla*, following Burn (1969).

Three species of *Aeolidiella*, *A. glauca*, *A. alderi*, and *A. sanguinea*, have been reviewed by Tardy (1969). Tardy demonstrated consistent differences between these taxa, which he considered significant enough to justify separation of these species previously placed in synonymy (Engel 1925). These three species all possess only two ceratal rows in the anterior digestive branch, rather than an elongate arch as suggested by Engel (1925) and Macnae (1954). All other species of *Aeolidiella*, where described, possess five or more rows in the anterior digestive system. Of the remaining species, *A. indica*, *A. orientalis*, *A. saldanhensis*, *A. hulli*, *A. takanosimensis*, *A. multicolor*, and *A. lurana* are strikingly similar in their morphology and a detailed comparison of these species is presented in Table 3.

Variation in colour has been adequately described only in *Aeolidiella multicolor* and *A. takanosimensis*. The latter appears to be more variable but is commonly decorated with red or orange pigment surrounding distinctive shapes of opaque white areas on the head and mid-dorsal region of the pericardium (Sphon 1971; Baba 1979). Alternatively, *A. takanosimensis* may rarely lack orange pigment or other dorsal markings (Gosliner 1980). Similar pattern distribution is found in *A. multicolor*. The latter species is far more consistent in its coloration and always bears a U-shaped area of orange pigment on the head and opaque or translucent white patches in the region of the pericardium, which resemble a 'Greek vase' (Eliot 1908). The above basic pattern of coloration has also been recorded in *A. orientalis* (Bergh 1890, pl. 86 (fig. 1);

Eliot 1908; Edmunds 1969), *A. hulli* (Risbec 1928, pl. 12 (fig. 4)), and *A. lurana* (Marcus & Marcus 1967, fig. 149). The coloration of *A. indica* was superficially described (Bergh 1888a) and there is nothing contradictory to that of the above species. *A. saldanhensis* (Barnard 1927) was described from preserved specimens and coloration was not given.

In all citations of the above species the rhinophores and masticatory border of the jaws are smooth and the foot corners are short. The two South African species *A. saldanhensis* and *A. multicolor* were separated by Macnae (1954) on the basis of the rounded foot corners reported in the former. However, in his drawing Barnard (1927: 201, fig. 2) indicated the presence of angular foot corners.

Where it has been described, the anterior digestive branch in all the above species consists of 5 to 7 oblique ceratal rows. The arrangement of the posterior digestive branches was used by Baba (1979) to distinguish *A. takanosimensis* from *A. multicolor* based on Macnae's (1954) account. However, the description by Macnae of the ceratal branching in *A. multicolor* is erroneous. Our examination of South African material has shown the ceratal configuration to be identical with that described for *A. takanosimensis* (Fig. 7A). The first three ceratal groups of the posterior digestive system of *A. lurana* were described as arches (Marcus & Marcus 1967) in an 8.5 mm specimen. The authors consider that these may be groups of two rows which in larger specimens may proliferate into additional rows. The branching of the posterior digestive system is incompletely described in *A. saldanhensis*, *A. indica*, *A. orientalis*, and *A. hulli*.

Examination of specimens of varying size shows that the radula of *A. orientalis* contains 9 to 25 teeth with 5 to 35 denticles on each side of the central denticle (Bergh 1888b; Eliot 1908; Edmunds 1969). The number of teeth and denticles of *A. indica*, *A. saldanhensis*, *A. hulli*, *A. takanosimensis*, *A. multicolor*, and *A. lurana* fall within the limits of this variability. Figure 10 shows the structure and variability of the radular tooth within and between species. Marcus & Marcus (1967) suggested that *A. multicolor* is distinct from *A. indica* on the basis of the radular tooth. However, at least the same degree of variability is shown in the drawings of the teeth of *A. takanosimensis* (Baba 1949, 1979; Ferreira & Bertsch 1975; Gosliner 1980).

Large oral glands have been described in *A. multicolor*, *A. takanosimensis*, and *A. hulli*, but have not been studied in *A. saldanhensis*, *A. indica*, *A. orientalis*, and *A. lurana*. The reproductive system has been described only in *A. multicolor* (Macnae 1954) and *A. takanosimensis* (Schmekel 1970) and they are entirely consistent with each other. The penis has been described for *A. orientalis* (Bergh 1888b) and is identical with that of the above two species.

The distribution of the above species under discussion (*A. indica*, *A. orientalis*, *A. saldanhensis*, *A. hulli*, *A. takanosimensis*, *A. multicolor*, and *A. lurana*) has been listed in Table 3. *Aeolidiella takanosimensis* has the widest recorded distribution. This pattern of wide-ranging, dispersed taxa is difficult to explain if they are considered as distinct species.

TABLE 3
Comparison of morphological characteristics of different species of *Aeolidiella*.

Species	Distribution	Colour	Jaw masticatory border	No. of radular teeth	No. of lateral denticles	Branching of digestive system		Foot corners	Oral glands	Reference
						anterior	posterior			
<i>A. glauca</i>	• Mediterranean, • England	white spots on body, rhinophores and oral tentacles, cerata pink to dark brown	smooth	18-20	25-30	2 rows	10 simple, single rows	short	unknown	Alder & Hancock 1845; Tardy 1969; Thompson & Brown 1976
<i>A. alderi</i>	• Mediterranean, • England	rhinophores white, yellow or orange, cerata rose-salmon or brown	smooth	18-20	25-30	2 rows	9 single rows	short	unknown	Tardy 1969
<i>A. sanguinea</i>	• Mediterranean	oral tentacles and rhinophores with opaque white and whole body coloured yellow-orange, rose or vermilion	smooth	18-20	25-30	2 rows	9 single rows	short	unknown	Tardy 1969
<i>A. multicolor</i>	• South Africa	white with orange and white pattern on dorsum, cerata orange and blue	smooth	15-22	17-32	6 to 8 rows	3 groups of 2-4, 2-3, 2-3 rows followed by 6 rows	short	large oral glands	Macnae 1954; present study
<i>A. saldanhensis</i>	• South Africa	unknown	smooth	24	24	unknown	unknown	short	unknown	Barnard 1927
<i>A. takanostimensis</i>	Japan, California, Mexico, Hawaii, Naples	variable; usually red- orange pigment sur- rounding opaque white pattern on dorsum; cerata red to brown, subapical white band	smooth	12-20	15-20	7 rows	4 groups of 4, 4, 3 and 2 rows followed by 5 rows	short	large oral glands	Baba 1949; Baba 1979; Schmekel 1970; Gosliner 1980

<i>A. drusilla</i>	· New Zealand	unknown	finely striated	21	23-25	unknown	unknown	short	large oral glands	Bergh 1900
<i>A. faustina</i>	· New Zealand	unknown	finely striated	25	35	unknown	unknown	unknown	unknown	Bergh 1900
<i>A. indica</i>	· Mauritius	white-yellow or green-yellow body, cerata grey or yellow	smooth	19-22	17-21	5 to 7 rows	first group has 2-3 rows followed by 8 rows	short	unknown	Bergh 1888a
<i>A. orientalis</i>	Red Sea, Indian Ocean, Tanzania	body translucent white dorsum red with white marks; apical part of rhinophores and oral tentacles red; cerata red-brown with subapical white bands	smooth	9-25	5-35	7 rows	14 rows	short	unknown	Bergh 1888b; Eliot 1908; Edmunds 1969
<i>A. hulli</i>	· New Caledonia	grey with white area over heart, cerata reddish-brown	smooth	15	24-30	unknown	unknown	short	large oral glands	Risbec 1928
<i>A. risbeci</i>	· Vietnam	unknown	smooth	15	35-40	unknown	unknown	short	large oral glands	Risbec 1956; Marcus 1961a; Burn 1969
<i>A. lurana</i>	· Brazil	white with pink, yellow, orange and opaque white pattern on dorsum, cerata orange with white subapical band	smooth	16	18-21	5 rows	3 groups of 2 rows each	short	unknown	Marcus & Marcus 1967
<i>A. occidentalis</i>	· St Thomas (West Indies)	unknown	smooth	15-19	28-30	unknown	unknown	unknown	unknown	Bergh 1874

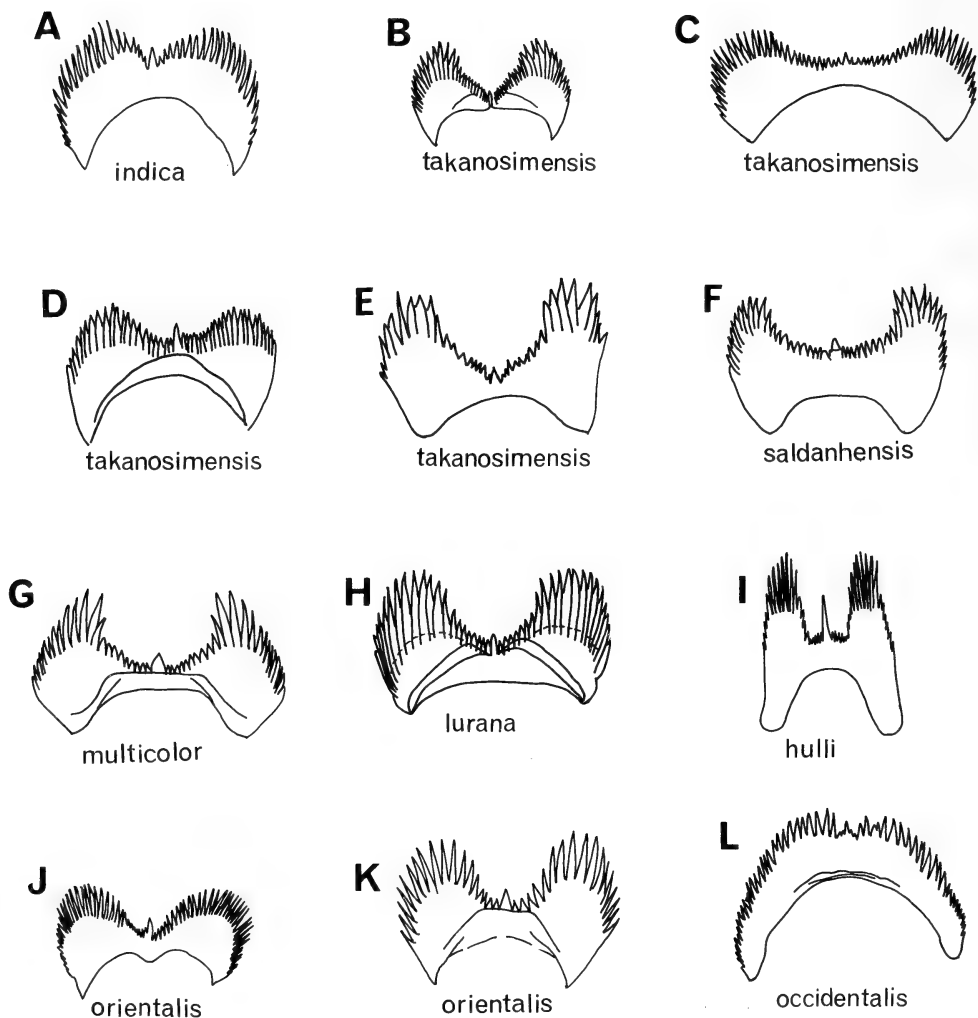


Fig. 10. Radular teeth of some species of *Aeolidiella*. A. *A. indica* (after Bergh 1888a). B. *A. takanosimensis* (after Baba 1949). C. *A. takanosimensis* (after Ferreira & Bertsch 1975). D. *A. takanosimensis* (after Baba 1979). E. *A. takanosimensis* (after Gosliner 1980). F. *A. saldanhensis* (after Barnard 1927). G. *A. multicolor* (after Macnae 1954). H. *A. lurana* (after Marcus & Marcus 1967). I. *A. hulli* (after Risbec 1928). J. *A. orientalis* (after Bergh 1888b). K. *A. orientalis* (after Edmunds 1969). L. *A. occidentalis* (after Bergh 1874).

Based on the above morphological and distributional comparison, we find as much variability for any single characteristic within a single species as between species. The similarity in coloration pattern, radular teeth and branching of the digestive system leads us to the conclusion that *A. orientalis*, *A. saldanhensis*, *A. hulli*, *A. takanosimensis*, *A. multicolor*, and *A. lurana* should be regarded as junior subjective synonyms of *A. indica* Bergh, 1888. The description of *A. indica* was published earlier in 1888 than that of *A. orientalis* and, therefore, has priority.

The descriptions of *A. risbeci* Marcus, 1961a, *A. occidentalis* Bergh, 1874, *A. faustina* Bergh, 1900, and *A. drusilla* Bergh, 1900, are incomplete and prevent meaningful comparison with *A. indica*.

Family Tergipedidae

Catriona columbiana (O'Donoghue, 1922)

Figs 1D, 11–12

Amphorina columbiana O'Donoghue, 1922: 160, pl. 6 (figs 23–24).

Cuthona alpha Baba & Hamatani, 1963a: 340, pl. 11. Williams & Gosliner, 1979: 214.

Cratena spadix MacFarland, 1966: 351, pl. 60 (fig. 4), pl. 68 (figs 12–17), pl. 69 (figs 6–7a).

Williams & Gosliner, 1979: 214.

Catriona columbiana (O'Donoghue, 1922), Marcus & Marcus, 1960: 179.

Catriona alpha (Baba & Hamatani, 1963a) Roller, 1969: 421.

Material

South African Museum, Cape Town

SAM-A34873, 1 m depth, Cape Town docks (33°54'S 18°26'E), 25 June 1972, 4 specimens.

Distribution

Japan (Baba & Hamatani 1963a), British Columbia (O'Donoghue 1922), California (MacFarland 1966), South Africa (present study).

External morphology

Several specimens were examined, the largest measuring 11 mm in length when alive (Fig. 1D). The foot is broad with anteriorly rounded corners. The oral tentacles are shorter than the rhinophores. The rhinophores are smooth and elongate and eye spots are visible at their posterior base. The distribution of cerata and digestive branches is shown in Figure 11A. The left and right anterior digestive groups each comprise 4 or 5 parallel rows of cerata. There are 6 posterior digestive branches per side which, except for the last row, branch alternately from the midline. During movement the cerata are characteristically carried flat over the back of the animal and may hang down over the lateral edges of the foot. The gonopores are ventral to the second and third ceratal rows of the right digestive group. The acleioproctic anus is situated in front of the inner corner of the second ceratal group and the nephroproct adjacent to the anus.

The general body colour is translucent white as are the cephalic tentacles and rhinophores (Fig. 1D). The cerata contain the light pink or yellow digestive gland and all are covered with a layer of opaque white epidermal pigment. This pigment also extends over the dorsum with a thick line between the rhinophores extending on to the front of the head, but not reaching the anterior margin. The oral tentacles bear an inner dorsolateral opaque white line down their length and the basal third of the rhinophores is speckled with white pigment. The middle of the rhinophores contains a broad transverse orange band, while the distal portion is densely opaque white.

Internal morphology

The jaws are fragile and elongate (Fig. 11C). The masticatory border (Fig. 11D) is thin and bears a row of strong bristles along the cutting edge. The radula (Figs 11B, 12) is long and thin with 80 teeth that become progressively larger and more developed towards the formative end. An elongate pre-radular tooth is present. The mature teeth have a receded median cusp and may or may not be flanked by 1 to 3 minute secondary denticles. There is usually a minute secondary denticle between the first and second lateral denticles.

The reproductive system (Fig. 11E) has a large bulbous ampulla on top of the genital mass. The albumen gland is small and closely associated with the membrane gland. The mucous gland is the largest portion of the female gland mass. The receptaculum seminis is attached by a short duct to the lateral side of the vagina. The proximal portion of the vas deferens is thickened and glandular, forming the prostate, while the distal end narrows and is closely folded against, and opens into, the penis. A large bulbous penial gland is present and the penis is elongate, conical and armed with a short stylet (Fig. 11F–G).

Natural history

Catriona columbiana was found crawling upon the ascidian *Ciona intestinalis* (Linnaeus) growing on wooden pilings in Table Bay docks.

Discussion

This species is discussed together with *Catriona casha* below.

Catriona casha sp. nov.

Figs 1E, 13–14

Material

Holotype

South African Museum, Cape Town

SAM-A34871, 1 m depth, Cape Town docks (33°54'S 18°26'E), 26 June 1972

Paratypes

SAM-A34872, 1 m depth, Cape Town docks (33°54'S 18°26'E), 26 June 1972, 5 specimens.

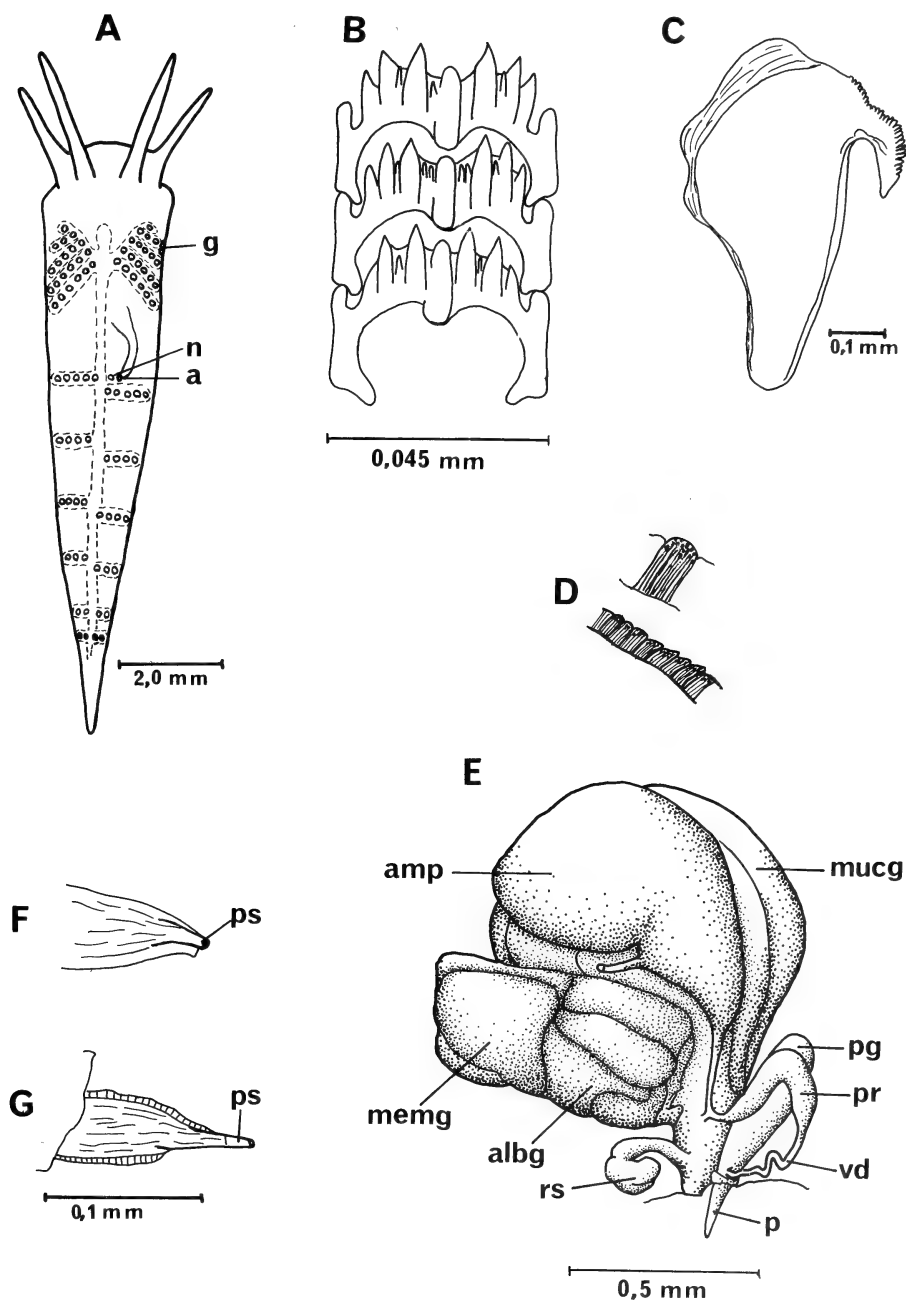


Fig. 11. *Catriona columbiana* (O'Donoghue, 1922). A. Dorsal view showing distribution of cerata and position of gonopores, nephroproct and anus. B. Radular teeth. C. Jaw. D. Detail of bristles of jaw. E. Reproductive system. F. Penis with retracted stylet. G. Penis with everted stylet.



Fig. 12. *Catriona columbiana* (O'Donoghue, 1922).
Scanning electron micrograph of the radula.
Scale: 10 μ m between squares.

Etymology

The word 'casha' is derived from Zulu, meaning to hide or conceal oneself and refers to the manner in which the cerata are carried horizontally, concealing the body.

External morphology

The live animals varied from 2 to 11 mm in length (Fig. 1E). They are small, somewhat stout with a broad anteriorly rounded foot. The rhinophores are smooth, stout and longer than the oral tentacles. A pair of eye spots is visible at the base of the rhinophores. The cerata are distributed in distinct transverse rows, 4 on each side of the anterior digestive group and 7 pairs of posterior rows (Fig. 13A). The cerata are fairly large and thick and droop on the ground as the animal crawls. When disturbed, the cerata bristle. The gonopores are below the second right ceratal row and the acleioproctic anus lies in front of the fifth ceratal row (Fig. 13A).

The body is translucent white with white internal organs visible through the body wall (Fig. 1E). The rhinophores and tentacles are also translucent white. The cerata contain a branch of the orange to orange-brown digestive gland and each bears a band of dense opaque white epidermal pigment at the distal end. Juvenile specimens show the same coloration pattern as the adults.

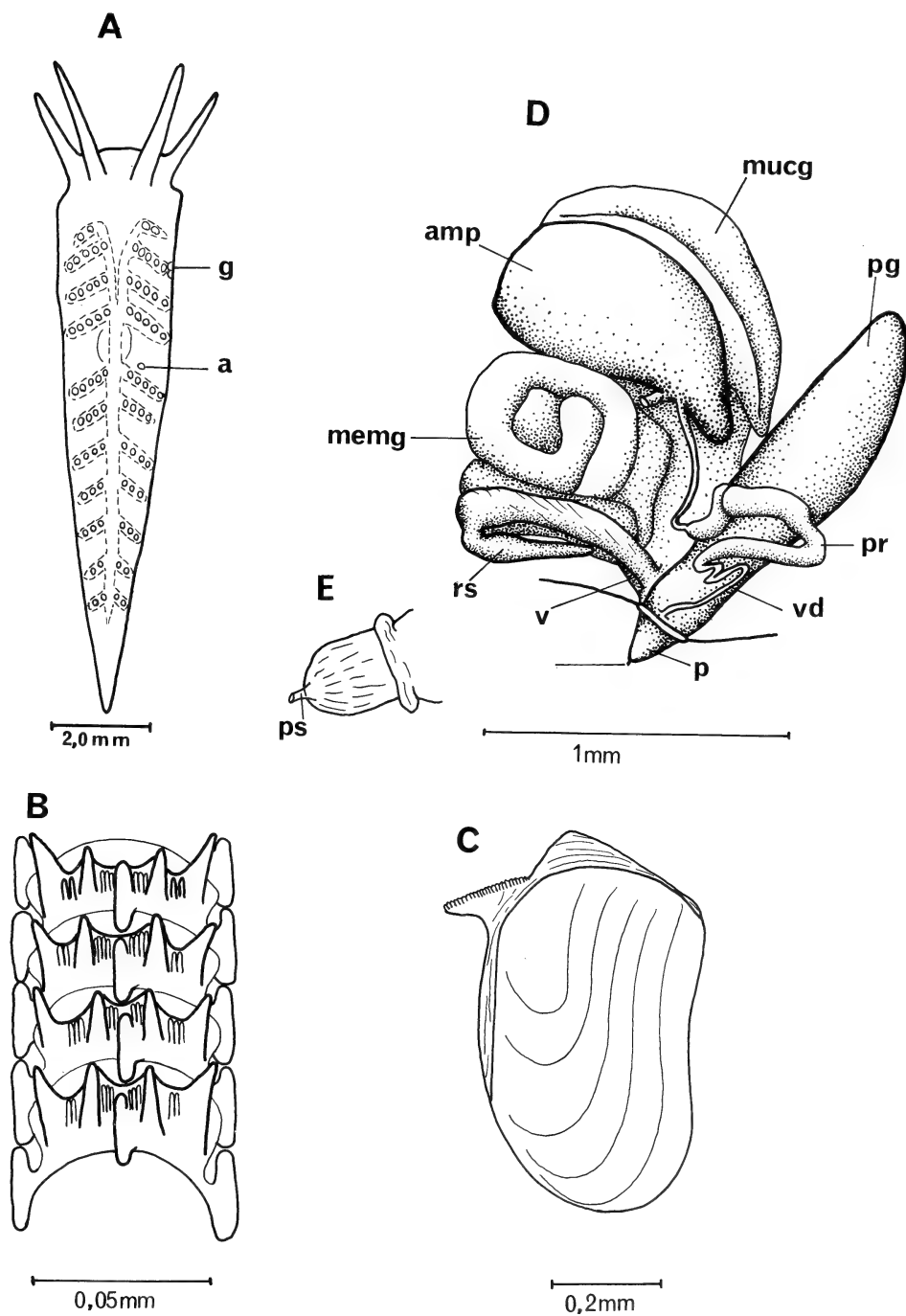


Fig. 13. *Catriona casha* sp. nov. A. Dorsal view of ceratal distribution and positions of gonopores and anus. B. Radular teeth. C. Jaw. D. Reproductive system. E. Penis showing penial stylet.

Internal morphology

The masticatory border of the jaw (Fig. 13C) bears a row of stiff bristles. The long tapering radula (Figs 13B, 14) has 76 teeth with an elongate pre-radular tooth. The teeth bear a receded central cusp and 2 large lateral denticles on either side. No variation in the number of large lateral denticles was observed, as seen in *Catriona columbiana*. There are 2 to 4 minute secondary denticles beside the central cusp and 2 or 3 between the lateral denticles. The tooth, therefore, bears more secondary denticles than that of *C. columbiana*.

The reproductive system is typically tergipedid. A large bulbous ampulla lies between the mucous and membrane glands (Fig. 13D). The post-ampullary duct from the ampulla is very thin. A glandular prostate forms the proximal portion of the vas deferens which narrows distally and becomes folded against the base of the large penial gland. The penis is conical and stout and bears a minute straight stylet (Fig. 13E). The receptaculum seminis is elongate and folded upon itself, with an enlarged, apparently glandular duct joining the vagina.

Natural history

Catriona casha has been found in association with the gymnoblastic hydrozoan, *Tubularia* sp., on which it presumably feeds.*

Discussion

The generic status of *Catriona* and *Cuthona* has been the subject of considerable controversy and has been reviewed by Burn (1973), Miller (1977), and Williams & Gosliner (1979). Although Miller (1977) suggested that there was no clear distinction between the two genera, Williams & Gosliner (1979) distinguished *Catriona* by the presence of bristles on the masticatory border of the jaw and the possession of more than 50 radular teeth which bear a quadrangular rather than an angular cutting edge. They also noted that the radula always bears a pre-radular tooth. These features are not common to members of the genus *Cuthona*. Williams & Gosliner suggested that the specimen upon which much of Miller's argument for joining the two genera is based, is not conspecific with *C. columbiana* (as *C. alpha* (Miller 1977)). This view is supported by examination of material from South Africa and is discussed below. Furthermore, examination of *Catriona casha* and *C. columbiana* from South Africa and comparison of these species with others in the genus confirm that the above characters (Williams & Gosliner 1979) remain distinctive to *Catriona*, with the possible exception of the absence of bristle-like denticles on the masticatory border of the jaw in the type material of *Catriona oba* (Marcus 1970; present study). The specimens described by Williams & Gosliner (1979) are probably not conspecific with *C. oba*.

Table 4 compares the distribution, colour and morphology of the different species assigned to the genus *Catriona* and Figures 15 and 16 illustrate the structure of the radular teeth and penial stylet. The coloration and morphology

* Additional data received while in press.

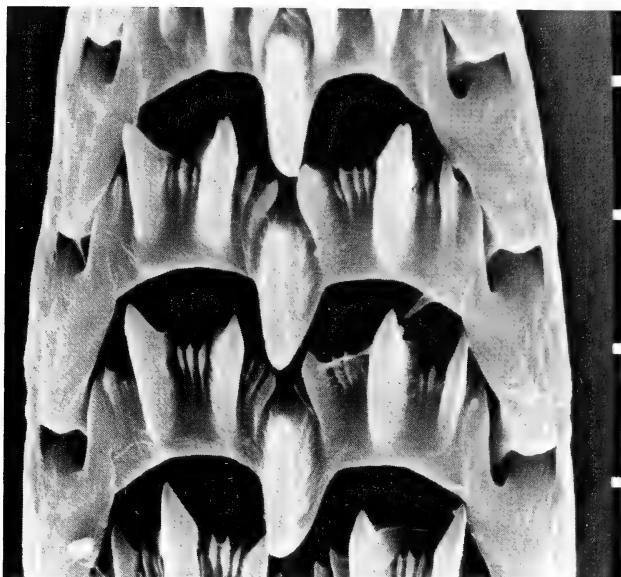


Fig. 14. *Catriona casha* sp. nov. Scanning electron micrograph of the radula. Scale: 10 μ m between squares.

of the South African specimens of *C. columbiana* agree closely with that of the holotype of *C. alpha* described by Baba & Hamatani (1963a) and Roller (1969), and there is little doubt that they are conspecific. Williams & Gosliner (1979) considered *C. alpha* (Baba & Hamatani 1963a) and *C. spadix* (MacFarland 1966) as junior synonyms of *C. columbiana* (O'Donoghue, 1922). Within the geographical range of *C. columbiana*, the cerata vary from pale yellowish-brown to light pink, orange, brown or vermillion with external opaque white over the whole surface or restricted to a white longitudinal line or subapical band on the cerata. The brighter coloured specimens (North America) have orange rhinophores and oral tentacles, while in the paler specimens (Japan, South Africa) the orange pigment is restricted to a band on the rhinophores. Although Williams & Gosliner (1979) stated that *C. columbiana* characteristically has only 2 large lateral denticles on the radular tooth, it should be noted that Baba & Hamatani (1963a) showed the possession of 2 or 3 denticles. South African specimens also possess 2 or more commonly 3 lateral denticles interspersed with 0, 1, or 2 minute denticles. The penial stylet in *C. columbiana* from South Africa is small and is visible only under high magnification. It is embedded in the tip of the elongate penis (Fig. 11F–G) and resembles that described for *C. columbiana* (MacFarland 1966, as *C. spadix*). The presence of a penial stylet in *C. columbiana* as *C. alpha* was not described by Baba & Hamatani (1963a), but was confirmed by Roller (1969). The shape of the penis (Baba & Hamatani 1963a, pl. 11 (fig. 6)) resembles that of the South African specimens. Regrettably the penis and stylet described by O'Donoghue (1922) were not illustrated.

TABLE 4
Comparison of the different species of *Catrina*. (PS) indicates information from present study.

Species	Distribution	Coloration	No. of teeth	Jaw border	Penis	Penial style	No. of rows in anterior digestive system	Reference
<i>C. gyrinota</i>	Northern Europe, U.S.A., Atlantic coast	orange rhinophores, orange to red cerata with distal white band and orange tips	68-81	bristles (PS)	elongate, conical (PS)	present (PS)	3-4 (PS)	Couthouy 1838; Alder & Hancock 1855; Gould & Binney 1870; Odhner 1939; Williams & Gosliner 1979; (PS)
<i>C. maui</i>	Florida, Naples	white on rhinophores and oral tentacles, head and back; rhinophores with posterior red line; cerata with 2 white longitudinal stripes, red to pale brown liver	80-120	bristles	elongate, conical	present	3-4	Marcus & Marcus 1960; Edmunds 1964; Schmckel 1968
<i>C. oba</i>	Brazil, Florida	rhinophores with red streak. 2 white lines on back; cerata pink with longitudinal white line	53	smooth (PS)	elongate, conical	present	2-3	Marcus 1970 (PS)
<i>C. tema</i>	Ghana	orange band on rhinophores; pigment on head and back, white subapical band and spots on cerata	137	bristles	short, conical	present	3	Edmunds 1968
<i>C. alpha</i> of Miller	New Zealand	white pigment on rhinophores, oral tentacles and back; subapical band on cerata; orange band on rhinophores; cerata light brown, pinkish tinge or fawn with green mottling	64	irregularly sinuate	very elongate	absent	3-4	Miller 1977
<i>C. columbiana</i>	British Columbia, California, Japan	rhinophores orange or orange band, white on oral tentacles, rhinophores, head, dorsum and cerata; cerata light vermillion, yellow or brown and may bear longitudinal white line, white line on oral tentacles	65-105	bristles	elongate, conical	present	5	O'Donoghue 1922; Baba & Hamatani 1963a; MacFarland 1966; Roller 1969; Williams & Gosliner 1979
<i>C. columbiana</i> (PS)	South Africa	rhinophores with orange band, white on head and back, white line on oral tentacles, dense white on cerata, cerata light yellow or pink	80	bristles	elongate, conical	present	4-5	(PS)
<i>C. casha</i>	South Africa	cerata orange with subapical dense white band; no other markings	76	bristles	short, conical	present	4	(PS)

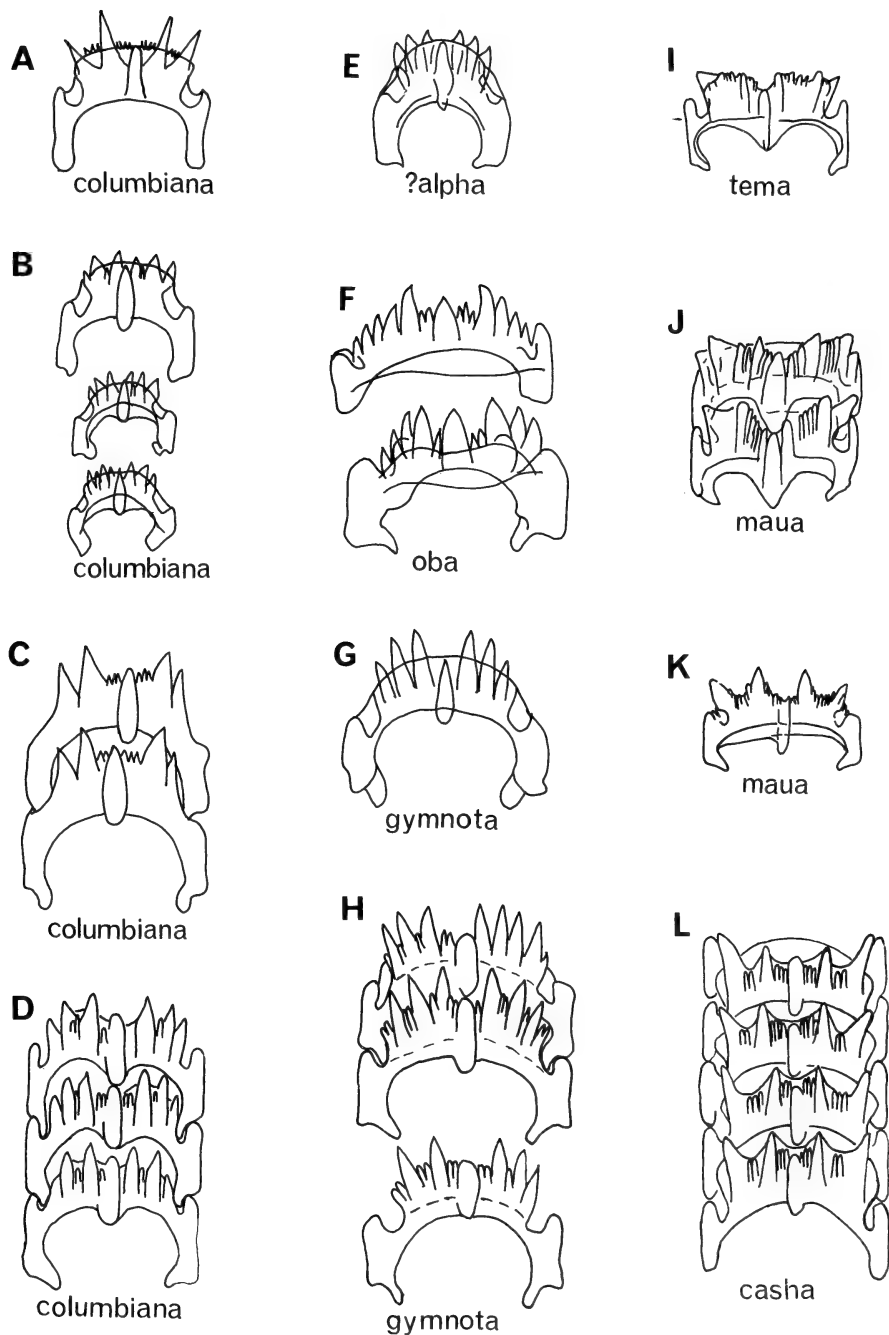


Fig. 15. Comparison of the radular teeth of *Catriona* species. A. *C. columbiana* (after O'Donoghue 1922). B. *C. columbiana* (after Baba & Hamatani 1963a as *Cuthona alpha*). C. *C. columbiana* (after MacFarland 1966 as *C. spadix*). D. *C. columbiana* (present study). E. ?*C. alpha* (after Miller 1977). F. *C. oba* (after Marcus 1970). G. *C. gymnota* (after Alder & Hancock 1855). H. *C. gymnota* (present study). I. *C. tema* (after Edmunds 1968). J. *C. maua* (after Marcus & Marcus 1960). K. *C. maua* (after Edmunds 1964). L. *C. casha* (present study).

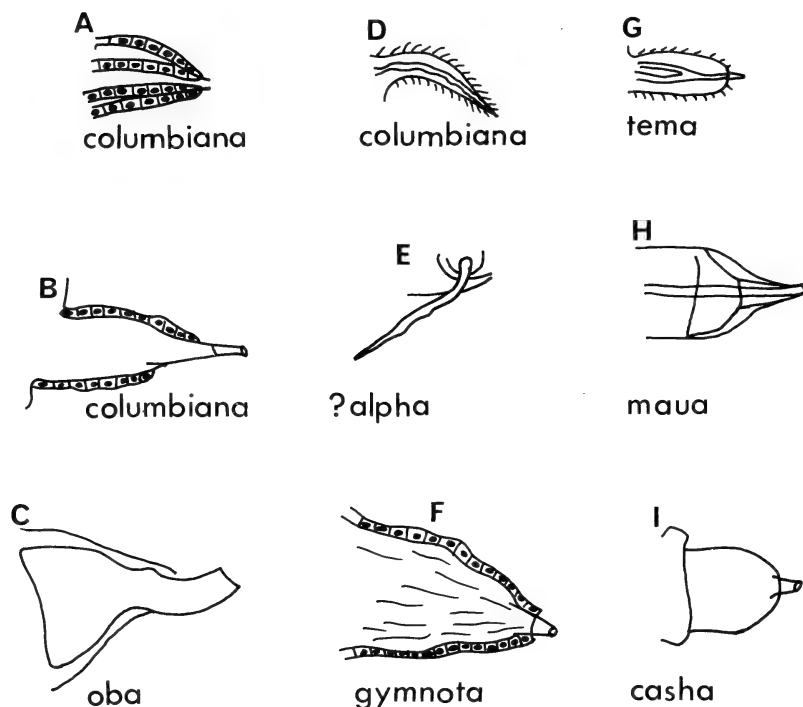


Fig. 16. Comparison of the penial papillae of *Catriona* species. A. *C. columbiana* (after MacFarland 1966 as *C. spadix*). B. *C. columbiana* (present study). C. *C. oba* (after Marcus 1970). D. *C. columbiana* (after Baba & Hamatani 1963a as *Cuthona alpha*). E. ?*C. alpha* (after Miller 1977). F. *C. gymnota* (present study). G. *C. tema* (after Edmunds 1968). H. *C. maua* (after Marcus & Marcus 1960). I. *C. casha* (present study).

The masticatory bristles on the jaws of South African specimens are large and clearly defined (Fig. 11D). The denticulation of the jaw of *C. columbiana* (O'Donoghue 1922, pl. 6 (fig. 23)) resembles that of the present material, although O'Donoghue did not distinguish their bristle-like structure. Roller (1969) confirmed the presence of bristles in Japanese and Californian material.

Based upon the similarities in coloration, radular teeth, jaws, penis and penial stylet, the present material is also considered to be synonymous with *C. columbiana* and closely resembles the Japanese material (Baba & Hamatani 1963a).

The status of New Zealand specimens identified as *C. alpha* by Miller (1977) remains uncertain. Although they may superficially resemble the description of *C. alpha* (Baba & Hamatani 1963a) as stated by Miller (1977), there are significant differences that require confirmation, particularly as the description of this species is now further amplified by the present study. Specimens described by Miller (1977) differ in that they have fewer ceratal rows in the anterior digestive branch, up to 4 lateral denticles in the radular tooth

instead of 2 to 3, a very elongate penis without a penial stylet and the absence of bristles on the masticatory border of the jaw.

Catriona casha agrees with other members of the genus in the possession of a long tapering radula bearing more than 50 teeth, a pre-radular tooth, a quadrangular cutting edge to the teeth and bristles on the masticatory border of the jaw. It differs from the other species of *Catriona* in the structure of the radular tooth and the shape of the penis and penial stylet. The tooth bears 2 major lateral denticles only, with 2 to 4 secondary denticles between the central and lateral denticles. South African *C. columbiana* have 2 to 3 large lateral denticles and have not been observed to possess more than 2 secondary denticles between the major ones. Most significantly, the penis of *C. casha* is stout and not elongate and tapering as in all other species of *Catriona* (Fig. 16). The penial stylet forms a small tube projecting from the rounded tip of the penis. The above differences are considered to be sufficient to warrant separate specific status.

Cuthona speciosa (Macnae, 1954)

Figs 1F, 17–19

Catriona speciosa Macnae, 1954: 4, figs 1–3, pl. 1 (figs 1–3).

Cuthona speciosa (Macnae, 1954) **comb. nov.**

Material

University of Cape Town, Department of Zoology

CP 818, 10 m depth, Castle Rocks, False Bay (34°14'S 18°29'E), 27 April 1973, 2 specimens

CP 791, intertidal, St James, False Bay (34°06'S 18°27'E), 30 March 1972, 1 specimen

CP 792, 2 m depth, Clovelly, False Bay (34°08'S 18°26'E), 10 September 1972, 1 specimen

CPR 94A, intertidal, Wilderness (34°00'S 22°33'E), 3 February 1973, 2 specimens

Other material

20 m depth, Llandudno (34°01'S 18°20'E), 15 December 1979, 2 specimens.

30 m depth, Vulcan Rock, Hout Bay (34°04'S 18°19'E), 20 January 1980, 1 specimen

Distribution

South Africa (Macnae 1954; present study).

External morphology

Live specimens (Fig. 1F) are up to 18 mm in length. The anterior margin of the foot is very slightly produced into tentacular processes. The stout oral tentacles are slightly shorter than the smooth, slender rhinophores. The cerata

are smooth and cylindrical and arranged in clearly recognizable rows with 2 to 4 rows per side in the anterior digestive branch. The posterior digestive branch has up to 7 rows per side. The gonopores are situated ventral to the second and third ceratal rows of the right side. The acleiproct anus is situated on the anterodorsal margin of the right posterior digestive branch. The nephroproct opens anterior to the anus.

The general body colour is yellow-orange, as are the cephalic tentacles and rhinophores, which may be decorated with pale pink pigment. The digestive gland within the cerata is dark brownish-green while the ceratal epithelium is yellow-orange and is covered either with bright luminescent blue or luminescent lilac pigment. In lilac-coloured specimens, the yellow cnidosac, visible in blue specimens, is obscured by opaque white pigment.

Internal morphology

The jaws (Fig. 17A) are thin and fragile. The masticatory border is smooth, without denticles. The uniseriate radula (Figs 18–19) has up to 64 teeth with 4 to 6 major denticles on each side of the central cusp. 1 or 2 secondary

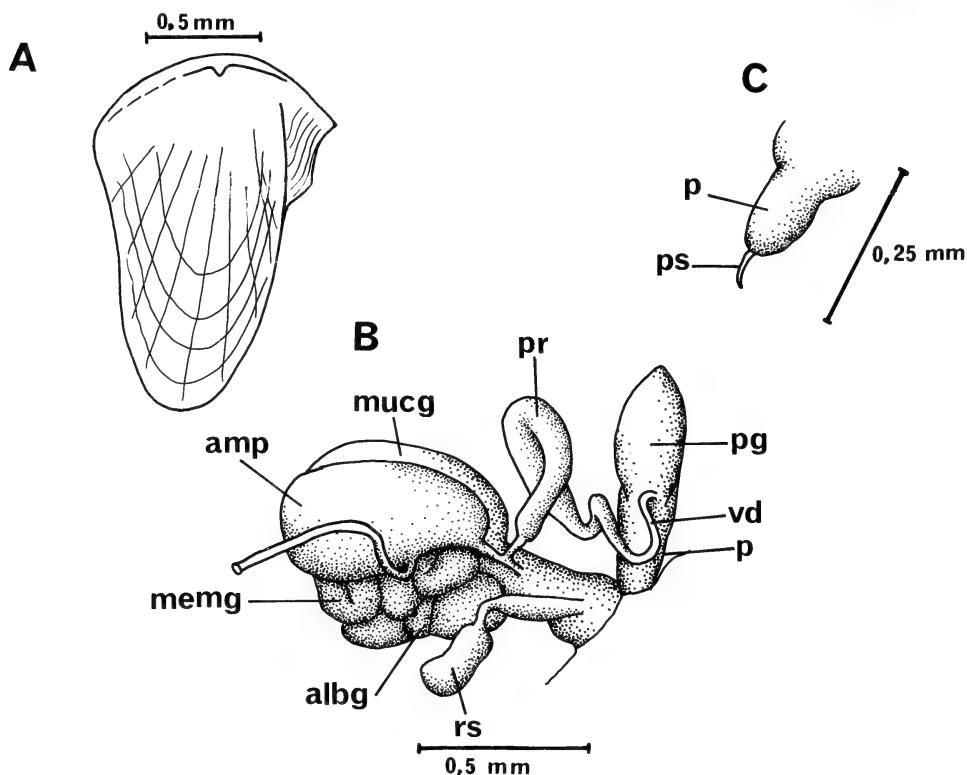


Fig. 17. *Cuthona speciosa* (Macnae, 1954). A. Jaw. B. Reproductive system. C. Penis showing penial stylet.

denticles may or may not be present between the central and first lateral denticle and between the first and second lateral denticles. The distribution of secondary denticles is highly variable within and between radulae.

The reproductive system (Fig. 17B) is similar to that described by Macnae (1954) but differs in three respects. There is no thin duct separating the penis from the penial gland; the penial stylet is slightly curved (Fig. 17C) and shorter than the penis; the prostatic vas deferens does not taper markedly into a non-prostatic portion.

Natural history

Cuthona speciosa is found on and feeds upon calyptoblastic hydrozoans of the genus *Sertularella*.*

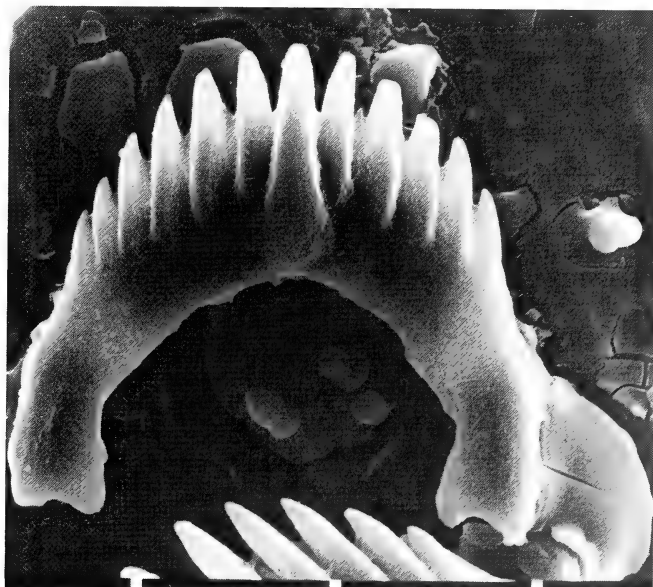


Fig. 18. *Cuthona speciosa* (Macnae, 1954). Scanning electron micrograph of radula. Scale: 30 μ m between squares.

Discussion

Macnae (1954) described *Catriona speciosa* from two specimens from False Bay, South Africa. The presence of a non-tapering radula and the absence of a pre-radular tooth indicate that this species is more properly placed in *Cuthona*, comb. nov. The present material agrees closely with that described by Macnae, but differs in several respects and encompasses a wider range of variation. The number of ceratal rows in the anterior digestive branch ranges from 2 to 4 and an increasing number of rows is not correlated with body size. Macnae described only 3 rows. The specimens described in this study were larger and

* Additional data received while in press.

more variable in their coloration and also had more radular teeth than previously described. They also differ from Macnae's specimens in that the jaws lacked denticles on the masticatory border. Variability in the general shape and structure of the radular teeth between specimens collected from different localities was a notable feature of the present material. Figure 19 illustrates the variability of this characteristic, which has not been adequately studied in other nudibranchs. Differences may be noted in the degree of arching of the base of the tooth, the size of the articulating surfaces, the relative sizes of the lateral denticles, the number of lateral denticles and the presence and position of the secondary denticles. In comparison with other specimens, the tooth of the animal shown in Figure 19D, as well as all other mature teeth in this radula, were considerably worn with blunt denticles. The two radular teeth which were still in the process of being formed bore typical elongate, sharp denticles.

Cuthona speciosa is thus more variable than previously described. The present material is, however, consistent with that described by Macnae (1954). The consistency of reproductive morphology in material from the present study suggests that discrepancies between this and Macnae's material (1954, fig. 3) are due to observational rather than morphological differences.

Family **Embletoniidae**

Embletonia gracilis Risbec, 1928

Figs 20–22

Material

South African Museum, Cape Town

SAM–A34874, intertidal, St James, False Bay (34°06'S 18°21'E) 1 January 1980, 1 specimen

SAM–A34875, intertidal, Clovelly, False Bay (34°08'S 18°26'E), 18 January 1980, 1 specimen

SAM–A34876, intertidal, St James, False Bay (34°06'S 18°21'E), 16 February 1980, 2 specimens

SAM–A 34877, intertidal, Clovelly, False Bay (34°08'S 18°26'E), 31 May 1980, 6 specimens

Distribution

New Caledonia (Risbec 1928), Japan (Baba 1959), Hawaii (Gosliner, 1980), Australia (Burn 1966), South Africa (present study).

External morphology

The elongate, slender animals reach a maximum length of 7 mm at maturity (Fig. 20). The animal is dorsoventrally compressed with the cerata held close to the body when actively crawling. The oral tentacles have been modified into a wide bilobed velum. The rhinophores are short and cylindrical.

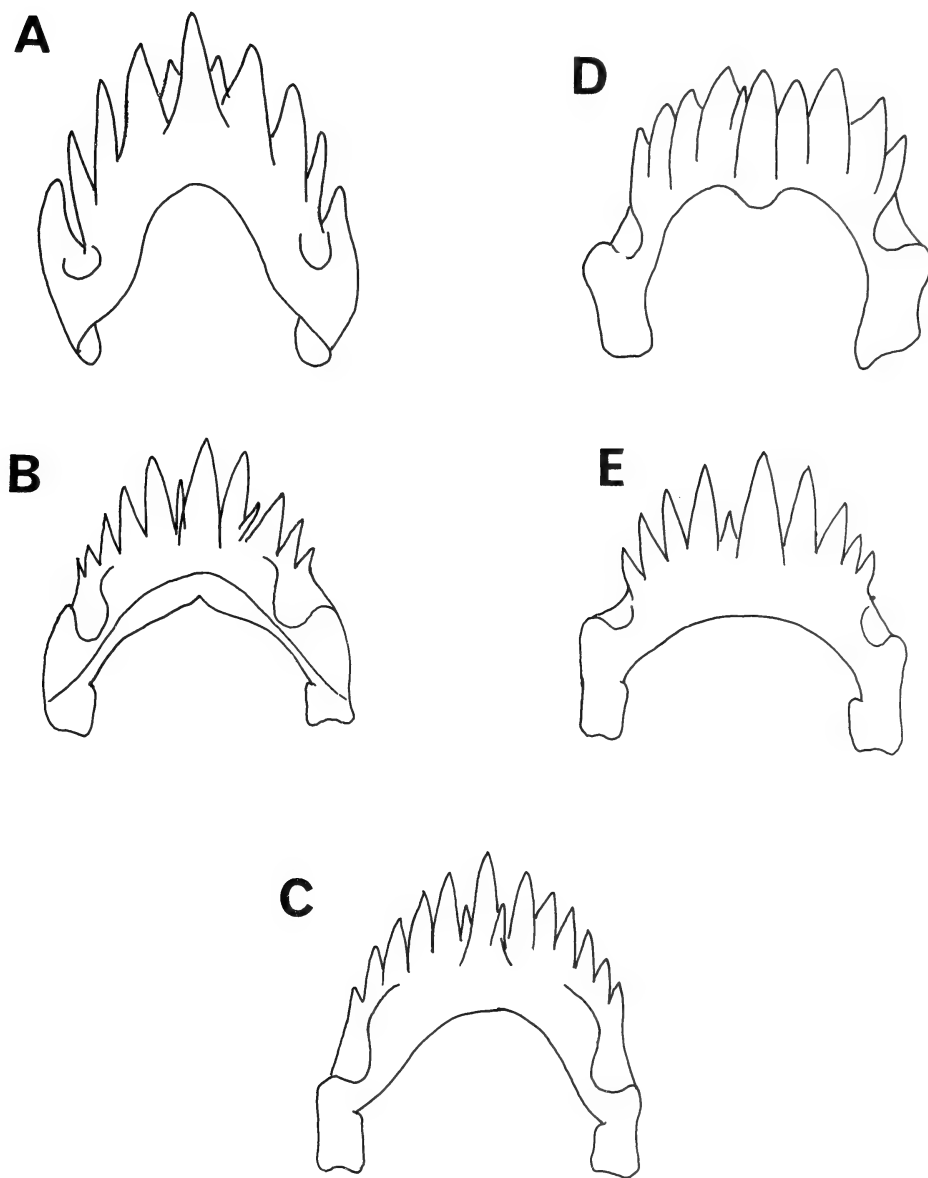


Fig. 19. Radular teeth of *Cuthona speciosa* (Macnae, 1954). A. False Bay (after Macnae 1954). B. Wilderness. C. Llandudno. D. St James, False Bay. E. Oudekraal. All specimens except C had blue cerata.

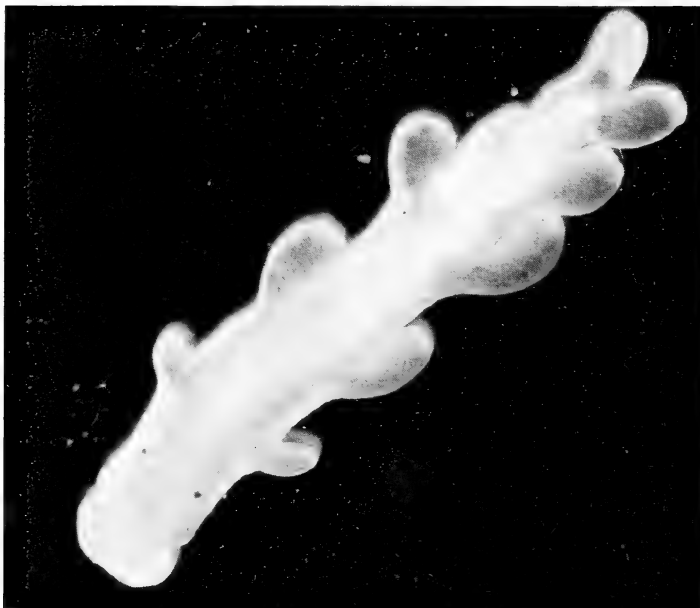


Fig. 20. *Embletonia gracilis* Risbec, 1928. Dorsal view of living animal at 20 \times magnification.

The anterior foot corners are simply rounded. The cerata are short and club-shaped, with four short and rounded cnidosacs on each ceras. When the animals are disturbed, the cerata elongate and four blunt apices are clearly visible. The cerata are arranged in 5 to 6 rows with a single ceras per row. There are 2 ceratal rows per side forming the anterior digestive branches. The pleuroproctus anus is situated immediately ventral to the notal brim in the interhepatic space, adjacent to the first ceras of the right posterior digestive branch. The separate male and female gonopores are located ventrally, between the first two cerata of the right side.

The living specimens are translucent white with salmon-pink digestive gland visible in the cerata and within the notum. In some specimens opaque white spots are present on the notum.

Internal morphology

The jaws (Fig. 21A) are elongate and delicate with a single row of 17 denticles along the slightly projecting masticatory border. The uniseriate radula contains 70 to 86 teeth. The teeth (Fig. 22) possess 2 to 4 denticles on each side of the equally prominent central cusp. The oral glands are well developed, as indicated by Baba and Hamatani (1963b) for *Embletonia gracilis paucipapillata*.

The reproductive system (Fig. 21B) consists of 6 to 8 hermaphroditic follicles that empty into the saccate ampulla. Distally, the ampulla narrows considerably and diverges into a short oviduct and a short non-prostatic vas

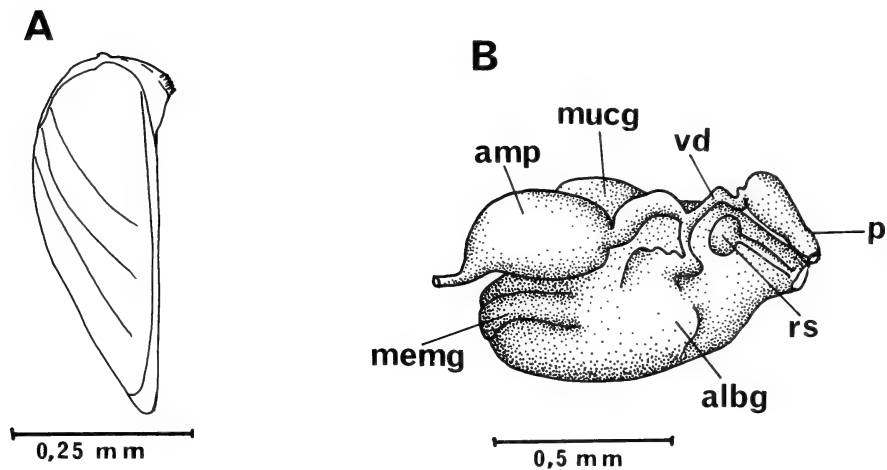


Fig. 21. *Embletonia gracilis* Risbec, 1928. A. Jaw. B. Reproductive system.

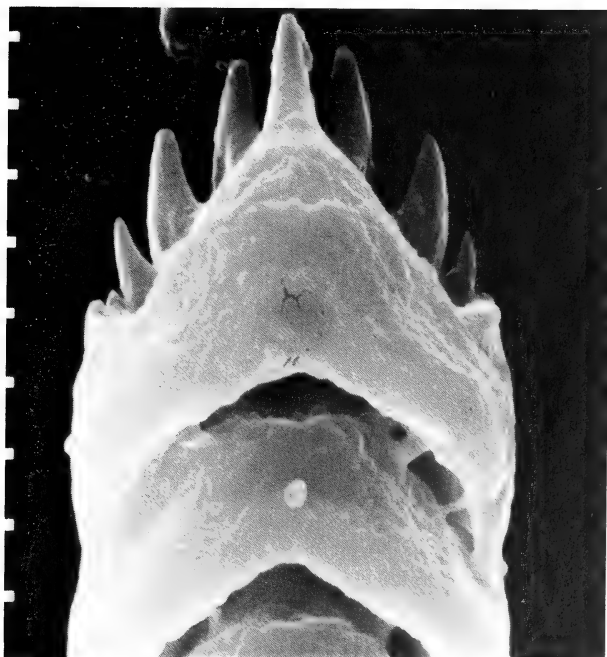


Fig. 22. *Embletonia gracilis* Risbec, 1928. Scanning electron micrograph of ventral view of radula.
Scale: 3 μ m between squares.

deferens, which expands into a prostatic portion. There is no distinct penial papilla or apical stylet. A receptaculum seminis is situated distally and joins the female gland mass at the female gonopore.

Natural history

Embletonia gracilis is associated with small colonies of intertidal campanularid hydroids, but has not been observed to feed upon them. *E. gracilis* lays a semicircular egg mass consisting of 4 to 19 eggs, with a single egg per capsule. This species undergoes direct development into a juvenile possessing four ceratal buds. From deposition of egg mass to hatching took 20 days at 20 °C.

Discussion

The genus *Embletonia* contains three or possibly four species. Its placement is questionable; some authorities placing it within the Dendronotacea (Miller 1977) while others (Marcus 1961*b*; Schmekel 1970) include it within the Aeolidacea. Marcus (1961*b*) stated that *Embletonia* is an aeolidacean genus, as the gonads are situated ventral to the digestive gland ducts. Miller (1977) stated that the Embletoniidae are more closely related to the Dendronotacea, although he provided no specific reasons. As the present material possesses ventral gonads, we consider the Embletoniidae as aeolids, closely allied to the Tergipedidae.

The type species of *Embletonia*, *E. pulchra* (Alder & Hancock, 1844), is known only from European waters. This species is characterized by a penis with a penial stylet, and a well-developed prostate (Marcus & Marcus 1958). *Embletonia faurei* Labbé, 1923, was described solely on the basis of external morphology, from two specimens collected from Brittany, France. Thompson & Brown (1976) considered *E. faurei* a junior synonym of *E. pulchra*. *E. faurei* has 9 cerata on each side of the animal (Labbé 1923) whereas there are 5 or 6 cerata per side in *E. pulchra*. The reproductive system of *E. faurei* was described by Schmekel (1970) and differs from that of *E. pulchra* (Marcus & Marcus 1958) in that a distinct prostatic portion is absent from the vas deferens. This appears to be a significant difference worthy of specific separation.

There remains some question as to whether the two species with an unarmed penis, which lacks a penial papilla, *E. gracilis* Risbec, 1928, and *E. paucipapillata* Baba & Hamatani, 1963*b*, should be regarded as distinct species. Both occur in Japan (Baba & Hamatani 1963*b*) and differ in their body shape, coloration, number of ceratal rows and degree of elaboration of the apical ends of their cerata. The specimens described from New Caledonia (Risbec 1928), Australia (Burn 1966), and South Africa (present study) are compared with the Japanese material in Table 5. The above specimens possess features that are intermediate between the Japanese forms, with the exception that deeply bifid ceratal apices are unique to specimens of *E. paucipapillata* from Osaka Bay. Additional material from other localities is required before a more definitive statement can be made with regard to the status of *E. gracilis* and *E. paucipapillata*.

TABLE 5
Comparative morphology of some species of *Embletonia*.

Specimens	Coloration	Ceratal rows	Ceratal apex	Body shape	Radula	Size	Reference
<i>E. gracilis</i> New Caledonia	white with grey digestive gland	7	with four blunt extensions	elongate, fusiform	c. 50 rows 3-4 denticles on each side of central cusp	5 mm	Risbec 1928
<i>E. gracilis</i> Japan	yellowish white, yellow digestive gland	7-8	with four blunt extensions	elongate, linear	72 rows 3 denticles on each side of central cusp	8 mm	Baba 1959; Baba & Hamatani 1963b
<i>E. gracilis</i> Australia	translucent white with opaque white patches, dull pink digestive gland	4-6	with four blunt extensions	short, fusiform	unknown	4.5 mm	Burn 1966
<i>E. gracilis</i> South Africa	translucent white, dull pink digestive gland	5-6	rounded, occasionally with four blunt extensions	elongate, fusiform	70-86 rows 2-4 denticles on each side of central cusp	4-7 mm	present study
<i>E. paucipapillata</i>	yellowish white, vivid orange digestive gland, opaque white on head and cerata	4-5	deeply bifid	short fusiform	80 rows 3 denticles on each side of central cusp	3-4 mm	Baba 1959; Baba & Hamatani 1963b

Of the specimens of *E. gracilis* previously described, the South African material most closely agrees with that described from Australia by Burn (1966). Our material differs from all described specimens of *E. gracilis* in that the apices of the cerata are normally rounded and exhibit the characteristic 'apical twigs' (Baba 1959) only when the animals are disturbed. It should be noted that, while the anal position of *E. gracilis* was described as acleioproctic (Baba & Hamatani, 1963*b*; Burn 1966), Baba & Hamatani's figure (pl. 17 (fig. 10)) clearly indicates that the anus is situated well below the notum (pleuroproctic) as in the present material.

Baba (1967) described the genus *Embletoniella* to include the two species of Embletoniidae with apical twigs in the cerata and an unarmed penis. Burn (1973) suggested that *Embletoniella* be regarded as a subgenus of *Embletonia*, at most. In material from this study the short apical twigs can be seen only when the cerata are fully extended. *Embletoniella* can be separated from *Embletonia* only by its absence of penial armature. This separation seems unnecessary as the closely allied genus *Cuthona* contains species with an armed and unarmed penis (Burn 1973). Therefore, we prefer to regard *Embletoniella* Baba, 1967, as a junior subjective synonym of *Embletonia* Alder & Hancock, 1851, syn. nov.

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ABBREVIATIONS

a	anus	og	oral gland
albg	albumen gland	p	penis
amp	ampulla	pg	penial gland
bc	bursa copulatrix	pr	prostate
cg	cerebral ganglion	ps	penial stylet
fgm	female gland mass	rh	rhinophore
g	gonopore	rs	receptaculum seminis
memg	membrane gland	s	stomach
mucg	mucous gland	v	vagina
n	nephroproct	vd	vas deferens

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae
Nuculana (Lembulus) bicuspidata (Gould, 1845)
Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
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T. M. GOSLINER
&
R. J. GRIFFITHS

DESCRIPTION AND REVISION OF SOME
SOUTH AFRICAN AEOLIDACEAN
NUDIBRANCHIA (MOLLUSCA, GASTROPODA)

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CAPE TOWN



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FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
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(continued inside back cover)

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CRAGIEVARUS KITCHINGI BRINK, 1965:
A SUBJECTIVE JUNIOR SYNONYM OF
DIADEMODON TETRAGONUS SEELEY, 1894
(REPTILIA, THERAPSIDA)

By

F. E. GRINE

Cape Town Kaapstad

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SYNONYM OF *DIADEMODON TETRAGONUS* SEELEY, 1894
(REPTILIA, THERAPSIDA)

By

F. E. GRINE

South African Museum, Cape Town

(With 11 figures and 2 tables)

[MS. accepted 4 December 1980]

ABSTRACT

The holotype of *Cragievarus kitchingi* has been re-examined. No other specimen has been referred to this taxon. The supposed diagnostic features of *Cragievarus kitchingi* are shown to be invalid; the type does not display morphology that serves to distinguish it from *Diademodon tetragonus*. Therefore, the name *Cragievarus kitchingi* Brink, 1965, is considered to be a subjective junior synonym of *Diademodon tetragonus* Seeley, 1894. The type specimen of *Cragievarus* is regarded as a subadult individual of *Diademodon tetragonus*.

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INTRODUCTION

The late Early to early Middle Triassic sediments of South Africa have yielded a large assemblage of moderately advanced, gomphodont cynodonts (Kitching 1977). The most commonly occurring forms in these deposits are a relatively homogeneous group of animals that has been placed in the subfamily Diademodontinae by Hopson & Kitching (1972).

Various diademodontine genera and species have been erected on often fragmentary remains from the late Early to early Middle Triassic sediments of South Africa and Zambia. Studies of cranial and dental morphology and analyses of the geographic and stratigraphic distributions of the diademodontine fossils have suggested that many, if not all, of the names that have been established (Table 1) are junior synonyms of *Diademodon tetragonus* Seeley, 1894 (Hopson 1971; Hopson & Kitching 1972; Kitching 1977; Grine 1977, 1978b). The results of allometric and multivariate statistical analyses of diademodontine crania have indicated that the specimens conform to a morphometri-

TABLE 1
Proposed synonyms of *Diademodon tetragonus* Seeley, 1894.

<i>Cynochampsia laniaria</i> *	. Owen, 1859
<i>Diademodon brachytiara</i>	. Seeley, 1894
<i>Diademodon mastacus</i>	. Seeley, 1894
<i>Diademodon browni</i>	. Seeley, 1894
<i>Gomphognathus kannemeyeri</i>	Seeley, 1895
<i>Gomphognathus polyphagus</i>	. Seeley, 1895
<i>Gomphognathus dimorphodon</i>	Seeley, 1908
<i>Diademodon entomophonus</i>	. Seeley, 1908
<i>Gomphognathus minor</i>	. Broom, 1911
<i>Diademodon platyrhinus</i>	. Broom, 1913
<i>Trirachodon browni</i>	. Broom, 1915
<i>Cyclogomphodon platyrhinus</i>	Broom, 1919
<i>Octagomphus woodi</i>	. Broom, 1919
<i>Protacmon brachyrhinus</i>	. Watson, 1920
<i>Gomphognathus grossarathi</i>	. Broili & Schröder, 1935
<i>Gomphognathus broomi</i>	. Broili & Schröder, 1935
<i>Gomphognathus haughtoni</i>	. Broili & Schröder, 1935
<i>Sysphinctostoma smithi</i>	. Broili & Schröder, 1936
<i>Protacmon reubsameni</i>	. Broom, 1950
<i>Diademodon parringtoni</i>	. Brink, 1955
<i>Diademodon laticeps</i>	. Brink, 1955
<i>Diademodon rhodesiensis</i>	. Brink, 1963
<i>Cragievarus kitchingi</i>	. Brink, 1965

*Application has been made to the International Commission on Zoological Nomenclature to conserve the name *Diademodon tetragonus* Seeley, 1894, with application of Articles 32a–b and 79 of the International Code of Zoological Nomenclature (Grine 1978a).

cally homogeneous group and that these crania represent an ontogenetic growth series of a single species (Grine & Hahn 1978; Grine, Hahn & Gow 1978; Bradu & Grine 1979).

Recently, however, Brink (1979) has proposed that the Diademodontinae comprises four species of *Diademodon*, viz. *D. tetragonus*, *D. mastacus*, *D. grossarathi*, and *D. rhodesiensis*, and an additional two generically separable taxa, *Sysphinctostoma smithi* and *Cragievarus kitchingi*.

The purpose of this paper is to evaluate the supposed diagnostic features and thus the taxonomic distinctiveness of *Cragievarus kitchingi* Brink, 1965. Whereas the species of *Diademodon* recognized by Brink (1979) are differentiated on cranial shape and proportions, and whilst *Sysphinctostoma smithi* is rediagnosed on supposed dental differences from *Diademodon* (Brink 1979), the diagnostic features of *Cragievarus kitchingi*, as will be shown below, are based on doubtful information and erroneous interpretations. Because of the peculiar problems presented by *Cragievarus kitchingi*, the type and only specimen of that taxon warrants detailed re-examination. Thus, *Cragievarus kitchingi* is dealt with here separately from the other supposed diademodontine taxa. The distinctiveness of the four *Diademodon* species recognized by Brink and the taxonomic validity of *Sysphinctostoma smithi* will be discussed in a future publication (Grine, in prep.).

MATERIAL AND METHODS

The holotype of *Cragievarus kitchingi* is in the collection of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, and is catalogued under Field Number 3776 and Museum Number 368. It was described by Brink (1965) and is the only specimen referable to that taxon (Brink 1979). It consists of an incomplete and rather poorly preserved skull found by J. W. Kitching in a 'fossil pocket' on the farm Cragievar, near Burgersdorp, Cape Province (Brink 1965; Kitching 1977). This small pocket also yielded a number of other diademodontine crania (Kitching 1963, 1977) that were referred originally to *Diademodon browni* (Brink 1963) and more recently to *D. grossarthi* (Brink 1979).

Recent examination of the type of *Cragievarus kitchingi* revealed a considerable amount of plaster of Paris reconstruction (Figs 3–5). The extent of this reconstruction was not readily apparent because the plaster had been painted to match the colour of the actual bone. The author has removed the plaster from the specimen and has performed some additional preparation, most notably in the removal of matrix from between the dentary and maxilla. Before any of this work was initiated, photographs, colour slides, and a silicone rubber mould of the specimen were taken; in addition, a plastic cast of the fossil, painted to resemble the specimen prior to cleaning, was made.

The original diagnosis, description and illustrations of the specimen were based upon the plaster reconstruction of the fossil (Brink 1965). In a later paper (Brink 1979), additions to the diagnosis of *Cragievarus kitchingi* and several quite significant modifications of the illustrative reconstruction of the specimen were made.

DESCRIPTION

As noted above, the purpose of this paper is to evaluate the supposed diagnostic features of the type of *Cragievarus kitchingi*, and as such a complete description of the specimen is not warranted. Rather, attention will be paid only to the features that have been stated (Brink 1965, 1979) as being peculiar to this specimen and as differentiating it from *Diademodon*. These characters are: (i) the delicate nature and shape of the temporal arch, (ii) the expansion of the ascending ramus of the dentary, (iii) the nature of the post-temporal fossa, (iv) the relative breadth of the braincase, (v) the height of the mid-sagittal parietal crest, (vi) tooth number, (vii) the length of the maxillary diastema, (viii) the replacement of the alisphenoid by the quadrate ramus of the pterygoid, and (ix) the divergence of the quadrate rami of the pterygoid.

Temporal arch

It has been stated that 'the peculiarity of the skull lies in the fact that it has the powerful extremely advanced lower jaw structure of a diademodontid. . . .

In sharp contrast, however, the zygomatic arch is delicate' (Brink 1965: 97). Furthermore, the arch of this specimen was considered to be a 'delicate, miniature *Diademodon*-like or *Trirachodon*-like arch, but it lacks evidence of a jugal process' (Brink 1965: 98). More recently, it was concluded that '*Cragievarus kitchingi* comes close to *Diademodon*, but it is best regarded as not a synonym because its zygomatic arches are conspicuously different (more slender, high, and less curved)' (Brink 1979: 7).

In both the 1965 and 1979 diagnoses of *Cragievarus kitchingi*, it was stated that the 'zygomatic arches [are] conspicuously reduced' (Brink 1965: 98, 1979: 43). To the later diagnosis was added that there is a 'weak jugal process (if any)'.

In an illustration of the right lateral side of the skull (Brink 1965) (Fig. 1 herein), a jugal flange is not present and the ventral border of the anterior portion of the jugal arch is drawn with a solid line, implying that this region is complete; posteriorly, the jugal-squamosal suture is represented intact with a suggestion that the posteroventral border of the squamosal is damaged; the squamosal crest is reconstructed as possessing a low, foreshortened profile. A later illustration, however, indicates that there might have been a slight jugal flange, and the squamosal crest is shown as having had a higher, posteriorly expanded profile (Brink 1979) (Fig. 2 herein). Here, too, the posteroventral border of the arch is represented as being relatively shallow but complete.

Comparison of Figures 3 and 4 (herein) indicates that the entire anterior portion of the temporal arch and the posterior parts of both the superior and inferior orbital borders are missing; thus, it is impossible to determine the size of the jugal flange because it is not preserved. In addition, the entire ventral border of the back of the arch (both the jugal and squamosal contributions) is damaged, and it is possible that this region extended further downwards for several millimetres.

The posterior crest of the squamosal is missing and has been illustrated as such (Brink 1965, 1979). The later reconstruction of this region (Fig. 2 herein) is considerably different from the earlier interpretation (Fig. 1 herein). Inasmuch as this part of the squamosal is not present in the original specimen, either (or neither) of the reconstructions could be correct. With a lack of concrete evidence indicating the configuration of a specific morphological feature, any reconstruction of it is hypothetical. It is particularly dangerous to incorporate such a reconstruction (e.g. the lack of, or the weak development of the jugal flange) into a taxonomic diagnosis.

The supposedly low degree of curvature, and the supposed slenderness and relatively delicate nature of the temporal arch of this specimen were considered to differentiate it from *Diademodon* (Brink 1965, 1979). The present author believes that these apparent features are artefacts of the damage that the arch has suffered. If the arch is extended ventrally in the front with the addition of a jugal flange and at the back with several millimetres of missing bone, then the supposedly straight contour and the delicate, slender appearance of the arch disappear.

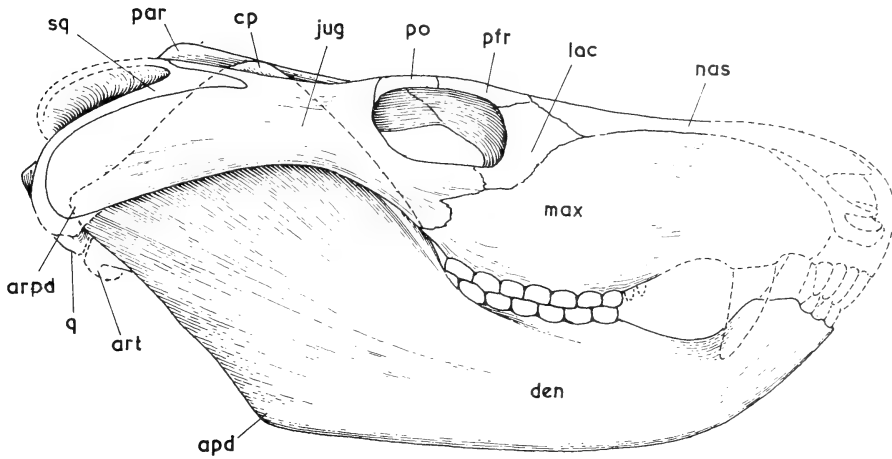


Fig. 1. Side view of the holotype of *Cragievarus kitchingi* as drawn by Brink (1965: 101, fig. 42).

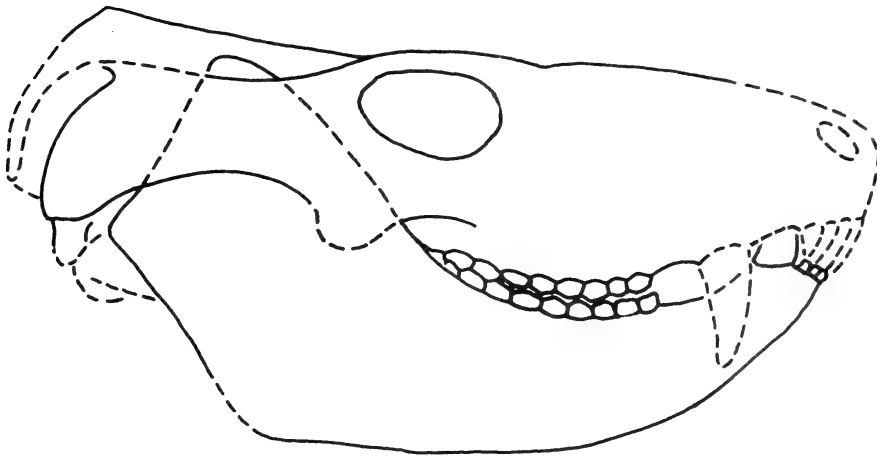


Fig. 2. Side view of the holotype of *Cragievarus kitchingi*, adapted from Brink (1979: 44).

Posterior expansion of the dentary

Brink (1965, 1979) stated that this specimen is 'diademodontid in general shape and structure, but with dentaries even more powerfully expanded posteriorly'. He noted the 'elaborate development' of the three portions of the ascending ramus of the dentary—the coronoid, articular and angular processes—and observed that 'the articular process reaches farther into the articular region and would appear to have had nearly direct contact with the squamosal' (Brink 1965: 105).

The earlier illustration of the dentary (Brink 1965, fig. 42) (Fig. 1 herein) shows the articular process of the dentary extending posterosuperiorly towards the squamosal, but in the later drawing (Brink 1979: 44) (Fig. 2 herein) this process is considerably foreshortened and does not reach even to the level of the inferior border of the temporal arch.

Examination of the specimen shows that the entire angular region of the dentary is missing from the right side (Fig. 4), but part of this region is preserved on the left side and it appears that the reconstruction of this region on the right is anatomically reasonable (Fig. 3). However, it is on the left side where the

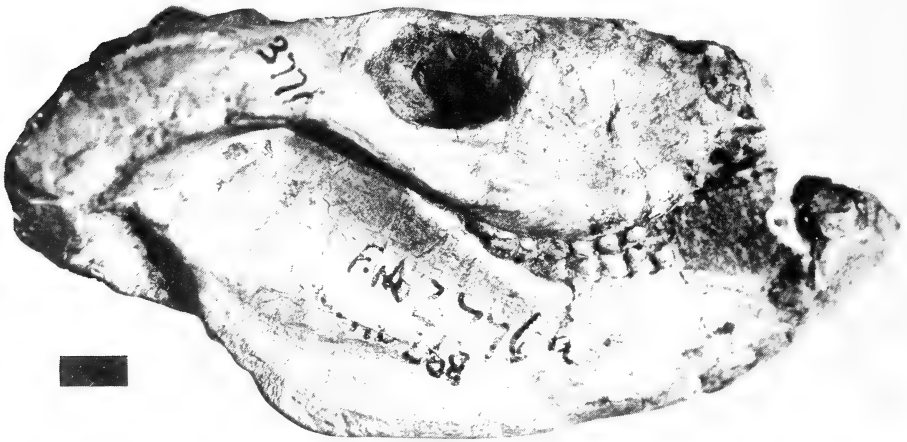


Fig. 3. Right lateral view of the holotype of *Cragievarus kitchingi* prior to the removal of the plaster (reconstructed) areas (cf. Figs 1–2, 4). Scale in cm.



Fig. 4. Right lateral view of the holotype of *Cragievarus kitchingi* after the removal of the plaster (reconstructed) areas and some of the matrix (cf. Figs 1–3). Scale in cm.



Fig. 5. Left lateral view of the holotype of *Cragievarus kitchingi* prior to the removal of the plaster (reconstructed) areas (cf. Fig. 6). Scale in cm.

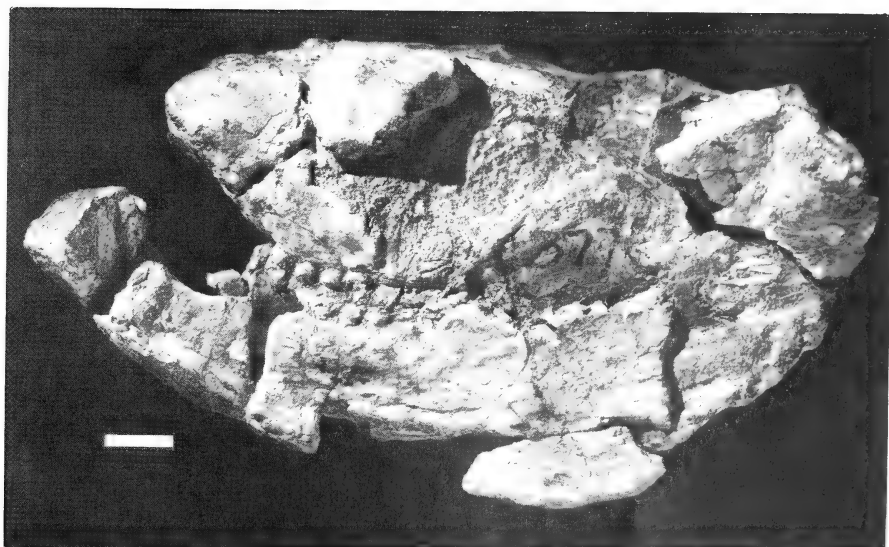


Fig. 6. Left lateral view of the holotype of *Cragievarus kitchingi* after the removal of the plaster (reconstructed) areas and some of the matrix (cf. Fig. 5). Scale in cm.

'powerful expansion' of the ascending ramus referred to and figured (Brink 1965, 1979) is best illustrated (Fig. 5). But here, too, much of the ascending ramus of the dentary has been reconstructed in plaster (cf. Figs 5-6). In fact, most of the left side of the cranium has been reconstructed, there being very little bone actually preserved.

Close examination of the left side of the specimen revealed an impression in the matrix of much of the inner surface of the ascending ramus of the dentary. Most notably, there exists the impression of part of the anterior margin of the ramus. The course of the anterior margin, as preserved as an impression, is at considerable variance with the course of this border in the plaster reconstruction (Fig. 7). The anterior margin of the dentary impression courses superoposteriorly, whilst in the reconstruction this border is considerably more vertically orientated. Over the lower third of the ramal height the plaster anterior margin is located about 6,0 mm in front of the actual (impression) border, and at a higher level the plaster margin is nearly 10 mm anterior to the margin of the impression. The mandibular reconstruction was modelled so that the anterior ramal margin met this margin as preserved on a piece of the tip of the coronoid process. However, this superior portion of the ramus is attached to a block of matrix that has been separated from the rest of the specimen (Fig. 6). There is no good contact between this block and the rest of the specimen, and it is evident that the tip of the ramus, as preserved on this piece, is positioned well out of normal anatomical alignment.

Thus, the 'powerful' expansion of the dentary ramus which was utilized in the diagnosis of *Cragievarus kitchingi* (Brink 1965, 1979), is based upon a reconstruction that departs from the original bony contours impressed in the matrix. Examination of the left and right mandibular rami of this specimen, in so far as they are preserved, indicates that they are expanded no more than in any *Diademodon* dentary of similar size.

Post-temporal foramen

It was originally claimed that 'a very peculiar aspect of this skull is to be found in the nature of the post-temporal fossa. On the right side the fossa is to be seen, on the side of the temporal vacuity, as a small shallow excavation extending directly inward in the direction of the brain case. On the posterior face there is only a depression with no sign of an opening. The region is not distorted to any degree so that an explanation cannot be sought in the fact that the opening has become closed through compression. The depression is situated below a distinct ridge extending from the dorsal border of the foramen magnum laterally and slightly upward, and it would appear as if a very small aperture was located here though no trace of it can be found' (Brink 1965: 102).

The next paragraph stated: 'To add to this very strange condition the post-temporal fossa, judging from the indication of it on the right forward side must have extended sharply laterally as it passed through from the posterior face

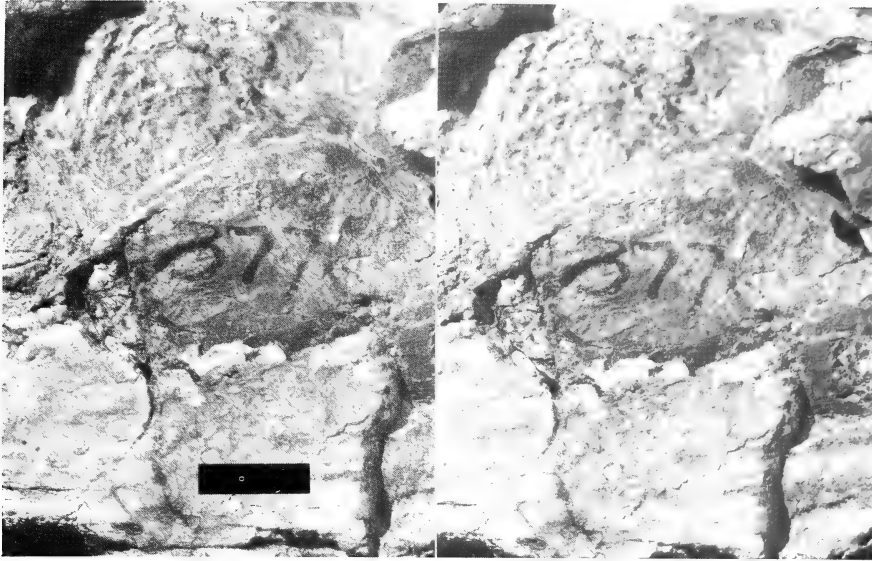


Fig. 7. Left side of the holotype of *Cragievarus kitchingi* showing the difference between the impression of the anterior border of the ascending ramus and the plaster reconstruction of the anterior border (white line) (cf. Figs 5–6). Scale in cm.

to the side of the temporal vacuity, but in both *Diademodon* and *Cynognathus* it extends inwards' (Brink 1965: 102).

The author finds it confusing that in the first of the two paragraphs quoted above the peculiar lack of a post-temporal foramen in this specimen was discussed at length, whilst in the second paragraph the peculiar course of the passage of this foramen was noted. It would appear that, although the openings of the post-temporal foramen could not be located, it was postulated that it opened anteriorly at the medial end of the 'small, shallow excavation' and posteriorly in the floor of the fossa bordering the foramen magnum. If this were the case, then the course of the canal's passage would be different from the direction it assumes in *Diademodon*.

Close examination of the back of this cranium revealed the presence of a matrix-plugged post-temporal foramen on the right side. The matrix that filled the foramen was carefully removed, and the foramen opens anteriorly where Brink (1965) suspected that it might. However, the posterior opening is considerably lateral to and above the level of the floor of the fossa where he postulated its exit to be (Fig. 8). This is the position normally occupied by this foramen in *Diademodon*, and it follows a nearly straight sagittal course as in *Diademodon*.

In a recent illustration of the occipital view of this specimen, Brink (1979: 44) indicated post-temporal foramina, and these are located in correct anatomical position, but an explanation of this new interpretation was not offered.

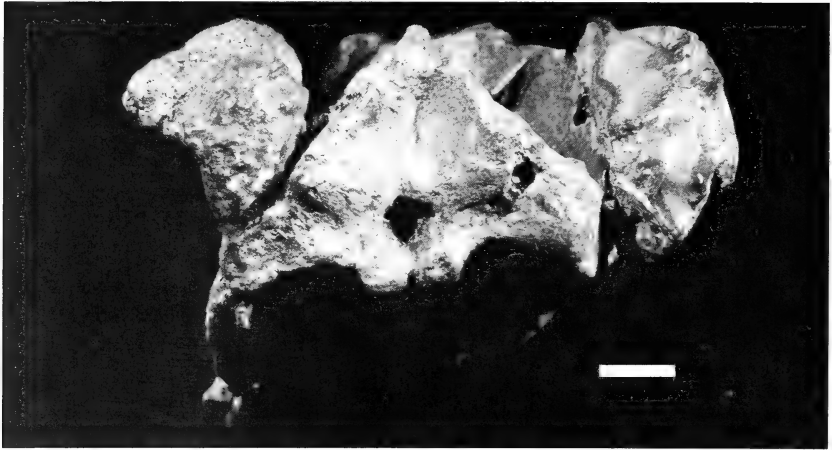


Fig. 8. Occipital view of the holotype of *Cragievarus kitchingi* showing the position of the right post-temporal foramen. Scale in cm.

Relative width of the braincase

In the original description of *Cragievarus kitchingi* (Brink 1965: 102), it was stated that 'proportionally the breadth across the braincase is greater than that of *Diademodon*'. At page 99 of the same paper, the maximum anterior and posterior breadths across the parietals were recorded as 17 mm and 10 mm respectively. However, comparable data for *Diademodon* upon which this assertion was based were not provided.

In the course of measuring *Diademodon* specimens for biometrical analysis, the present author has recorded the breadth of the parietals at the level of the pineal foramen (in an attempt to standardize this measurement) on a number of crania (Table 2). This measurement ranges between 6 and 25 mm in *Diademodon*; it is 14 mm in the type, and only specimen of *Cragievarus kitchingi*. The length of the cranium, from the level of a line tangential to the anterior border of the orbits anteriorly to the level of a line through the occipital condyles posteriorly, was measured also. This measurement, referred to as 'pre-orbital basal length' in previous studies (Grine & Hahn 1978; Grine, Hahn & Gow 1978; Bradu & Grine 1979), ranges between 21 and 158 mm in the present *Diademodon* sample; it is 61 mm in the type of *Cragievarus kitchingi*.

Comparison of 'pre-orbital' cranial length and parietal breadth in the present *Diademodon* sample (Fig. 9) indicates that, whilst the skull undergoes considerable ontogenetic elongation, there is little increase in the breadth of the brain-case with age. One *Diademodon* cranium in this sample (BPI.FN. 3773, one of the four *Diademodon* crania described by Brink (1963) from the Cragievar fossil pocket) has a 'pre-orbital basal length' which is the same as the type of *Cragievarus kitchingi*. The parietal breadth of the latter specimen is only 2 mm greater than that of the former.

TABLE 2

Measurements of cranial length, parietal breadth and indices of relative parietal breadth in diademodontine specimens of various sizes.

Catalogue no.	Length	Parietal breadth	Index	Previous taxonomic designation
BPI.FN. 3511 . . .	21	6	28,57	<i>Diademodon browni</i>
Munich 1936 II 8 . . .	32	8	25,00	<i>Sysphinctostoma smithi</i> (T)
BPI.FN.3756 . . .	36	12	33,33	<i>Diademodon mastacus</i>
BPI.FN. 3771 . . .	44	10	22,73	<i>Diademodon</i> sp.
BPI.FN. 3769 . . .	52	8	15,39	<i>Diademodon browni</i>
BPI.FN. 3776 . . .	61	14	22,95	<i>Cragievarus kitchingi</i> (T)
BPI.FN. 3773 . . .	61	12	19,67	<i>Diademodon browni</i>
Camb. T. 435 . . .	69	10	14,49	? <i>Protacmon</i> sp.
Munich 1934 VIII 14 . . .	72	12	16,67	<i>Gomphognathus ?browni</i>
Camb. T. 462 . . .	76	13	17,11	<i>Protacmon brachyrhinus</i> (T)
SAM - 1332 . . .	84	14	16,67	<i>Diademodon mastacus</i>
BMNH R. 3587/3588 . . .	84	14	16,67	<i>Gomphognathus minor</i> (T)
BMNH R. 3765/4092 . . .	86	13	15,12	<i>Diademodon entomophonus</i> (T)
BPI.FN. 3758 . . .	86	13	15,12	<i>Diademodon browni</i>
Munich 1934 VIII 15 . . .	92	13	14,13	<i>Gomphognathus</i> cf. <i>mastacus</i>
UCL. K. 11 . . .	100	14	14,00	<i>Diademodon</i> sp.
BMNH R.2578 . . .	103	14	13,59	<i>Diademodon polyphagus</i>
SAM - 5716 . . .	104	15	14,42	<i>Diademodon</i> sp.
BPI.FN. 4669 . . .	108	18	16,67	<i>Diademodon</i> sp.
Munich 1934 VIII 16 . . .	109	17	15,60	<i>Gomphognathus</i> cf. <i>mastacus</i>
Munich 1934 VIII 30 . . .	111	13	11,71	<i>Gomphognathus</i> cf. <i>mastacus</i>
USNM 23352 . . .	115	18	15,65	<i>Diademodon mastacus</i>
BPI.FN. 3639 . . .	118	21	17,80	<i>Diademodon rhodesiensis</i> (T)
Camb. T. 434 . . .	122	14	11,48	<i>Diademodon ?mastacus</i>
SAM - K. 5222 . . .	128	20	15,63	<i>Gomphognathus polyphagus</i>
Munich 1934 VIII 18 . . .	133	15	11,28	<i>Gomphognathus broomi</i> (T)
Munich 1934 VIII 17 . . .	142	17	11,97	<i>Gomphognathus grossarthi</i> (T)
Munich 1934 VIII 19 . . .	143	25	17,48	<i>Gomphognathus haughtoni</i> (T)
Camb. T. 436 . . .	149	17	11,41	<i>Diademodon laticeps</i> (T)
BPI. FN. 3754 . . .	158	23	14,56	<i>Diademodon grossarthi</i>

BPI.FN. = Bernard Price Institute for Palaeontological Research, Johannesburg

Munich = Bayerische Staatssammlung für Paläontologie, München

Camb. = University Museum of Zoology, Cambridge

SAM = South African Museum, Cape Town

BMNH = British Museum (Natural History), London

UCLZ = University College of London, Zoology Dept.

USNM = United States National Museum, Washington

(T) = holotype

An index of relative parietal breadth was calculated for each specimen according to the simple formula,

$$I = \frac{B}{L} (100)$$

where B is the breadth across the parietals and L is the 'pre-orbital basal' cranial length. The indices (Table 2) range between approximately 11,3 and 33,3 per cent of cranial length. When the index values are plotted as a function of 'pre-orbital' cranial length (Fig. 10), it becomes readily apparent that the

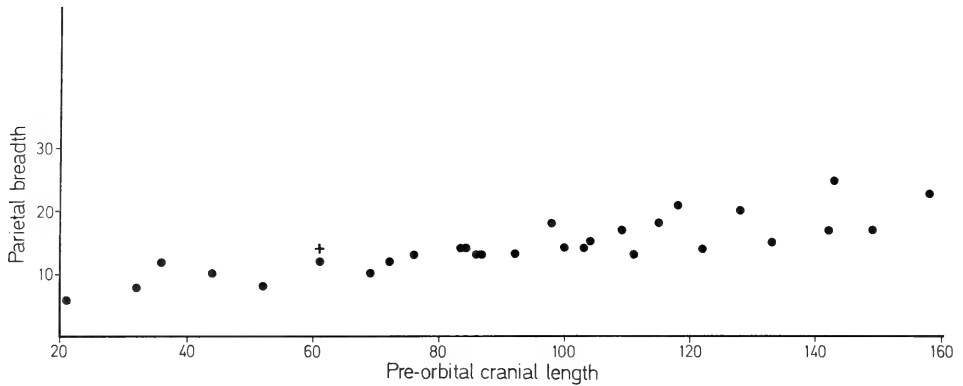


Fig. 9. Parietal breadth plotted as a function of cranial length in *Diademodon*. + = *Cragievarus kitchingi*. Scales in millimetre intervals. Note the slight increase in parietal breadth compared to the increase in cranial length.

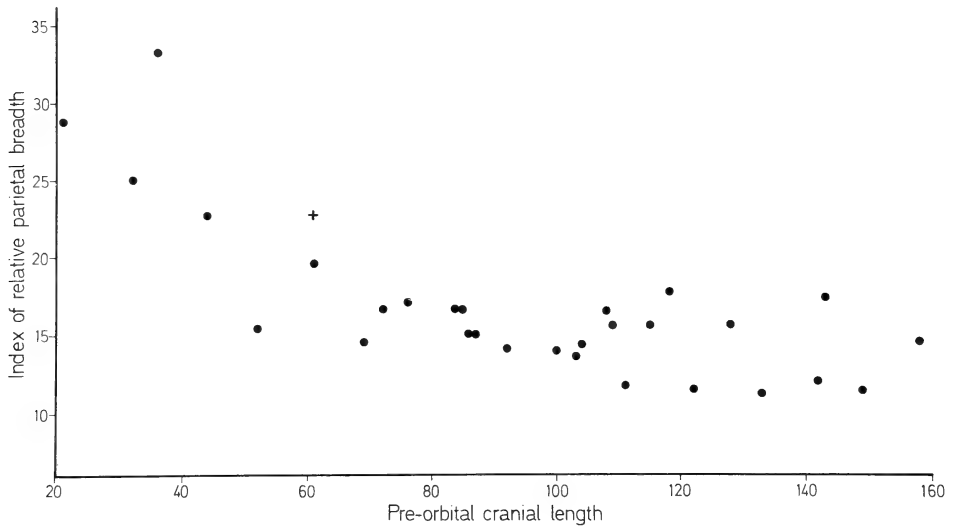


Fig. 10. Relative parietal breadth plotted as a function of cranial length in *Diademodon*. + = *Cragievarus kitchingi*. Ordinate scale in millimetre intervals, abscissal scale in percentage intervals. Note the relatively greater parietal breadth of the smaller (ontogenetically younger) crania.

relative parietal breadth decreases, in an apparently exponential manner, as cranial length increases. The index of relative parietal width for *Cragievarus kitchingi* has a value of 22,95 per cent, which is slightly greater than that shown by BPI.FN. 3773 (19,67 per cent). But the relative width of the braincase of the smaller (ontogenetically younger) *Diademodon* specimens appears to be rather variable (Fig. 10), and the relative parietal width of *Cragievarus kitchingi* fits comfortably into the *Diademodon* 'growth velocity' curve.

In their preliminary study of relative growth in the cranium of *Diademodon*, Grine, Hahn & Gow (1978) noted that the variables related directly to the size of the brain (parietal width) and orbits exhibit definite negative allometry compared to total cranial length. This phenomenon may be expected in an ontogenetic growth series, as it is well known that in vertebrates the brain and eyes of younger (juvenile) individuals are relatively larger than in older (adult) individuals. Thus, the relatively broad diameter of the braincase of *Cragievarus kitchingi* is not abnormal when the specimen is considered in an ontogenetic context as one of the smaller (younger) *Diademodon* specimens present in the currently available sample (see Table 2 and Figs 9–10).

Height of the mid-sagittal parietal crest

In the description of *Cragievarus kitchingi*, it was stated that, 'in both *Diademodon* and *Cynognathus* . . . the parietals have a greater height at the level of the prootic than farther forward at the level of the alisphenoid. In the present specimen the height is greater in front' (Brink 1965: 102–103). However, examination of the original specimen reveals that the mid-sagittal crest has been broken away from the back of the skull to the level that Brink (1965) regarded as its highest point.

Dental formula

In the original description of the present specimen, it was noted that in the maxilla 'there are indications of sockets of two very small evidently conical teeth, at the front of the postcanine series . . .' (Brink 1965: 103). According to this 1965 diagnosis, this specimen possesses four incisors, one canine, two conical teeth and seven molariform teeth on each side of the upper jaw, and three incisors, one canine, no conical teeth and seven molariform teeth on each side of the lower jaw. The original illustration (Brink 1965, fig. 32) (Fig. 1 herein) shows the dental formula diagnosed for this specimen. In the later diagnosis of *Cragievarus kitchingi*, the presence of 'seven "molariform" cheek teeth, with indirect evidence of conical teeth anteriorly, [and] even less evidence of sectorials posteriorly' was noted (Brink 1979: 43). However, in the later illustration of this fossil (Brink 1979: 44) (Fig. 2 herein) eight maxillary and eight (? possibly nine) mandibular molariform teeth are depicted. Even if one allows that the two maxillary conical teeth were inadvertently represented as a single molariform tooth, this same allowance cannot be made for the lower jaw, for according to Brink's (1965) own diagnosis there are no mandibular conical teeth present.

It is not possible to either substantiate or refute the claim that the specimen possessed four incisors on either side of the upper jaw (Brink 1965), as the entire anterior end of the rostrum is missing. While it is conceivable that this number may be correct, it cannot be demonstrated, and therefore it cannot be used in a taxonomic diagnosis. Similarly, the anterior end of the mandibular symphysis is covered in matrix and without its removal the number of incisive alveoli cannot be determined accurately.

There is only a single canine on either side of the lower jaw and the broken alveolus of the left maxillary canine is preserved. The alveolus and root of the upper canine became visible after the matrix and plaster that covered them were removed.

As Brink (1965) noted, there are two alveoli preserved anterior to the first (preserved) molariform tooth in the right maxilla; this region on the left side is damaged. Because of the relatively small diameters of these two alveoli, it seems reasonable to assume, as did Brink, that they contained conical teeth.

On the right side there is a break through the dentary in front of the first (preserved) molariform tooth (Fig. 4). Immediately anterior to this break there is a small, circular alveolus. This was not visible previously because the region was covered in matrix. The relevant portion of the left dentary is missing. It would appear that the lower jaw supported at least one conical tooth in front of the molariform series.

Seven maxillary molariform teeth are preserved on the right side, and at least five mandibular molariform teeth are visible on this side. On the internal aspect of the right dentary, the crowns of seven mandibular molariform teeth have been exposed; the lateral aspects of the crowns of the last two teeth are covered by matrix. On the right exterior the area behind the last visible molariform teeth is covered by matrix.

On the left side, however, there are eight post-conical teeth in both the maxilla and mandible. The teeth are visible from the external aspect only, and some of the crowns have been damaged. The last few teeth were covered by the plaster used in the cranial and mandibular reconstructions (cf. Figs 5–6). Although the posterior teeth are damaged, it is evident that the last mandibular and probably the last maxillary crowns are those of sectorial teeth.

In addition, removal of the plaster from the left side revealed two additional crowns behind the eighth mandibular tooth. The crowns of these last two teeth, although damaged, are mesiodistally elongate and buccolingually compressed. They appear to be sectorial teeth also. Because of their position and orientation it seems that these last two teeth had probably not yet erupted at the time of death of this individual.

Thus, according to the evidence provided by the prepared specimen, it appears that the maxilla contained perhaps two conical teeth, seven molariform teeth and one sectorial tooth, and that the mandible supported at least one conical tooth, seven molariform teeth and one sectorial tooth. Also, it is evident that there are at least two sectorial teeth contained in the dentary behind the sectorial tooth noted above; it appears that these latter two teeth had not yet erupted at the time of death.

The postcanine dental formula indicated above may be incorrect in so far as the numbers of the various postcanine tooth types are concerned, but it has been pointed out elsewhere (Grine 1977, 1978*b*; Grine, Hahn & Gow 1978) that in view of the type of replacement exhibited by *Diademodon*, postcanine tooth number is of limited diagnostic importance.

The diagnostic statement that there is 'indirect evidence of conical teeth anteriorly, and even less evidence of sectorials posteriorly' (Brink 1979: 43) is shown to be erroneous following a re-examination of the type specimen. Whilst the presence of conical teeth is inferred from alveoli, the actual crowns of the sectorial teeth are present.

Maxillary diastema

In the earlier description of the present specimen (Brink 1965: 103) it was stated that, 'there are indications of sockets of two very small evidently conical teeth, at the front of the postcanine series, with an unusually extensive diasteme separating them from the approximate position of the canine. The diasteme is actually preserved for a distance of fourteen millimetres in which there is no trace of a socket, even of a tooth long since lost, and this distance is reflected in the figures, but as there is no sign of the canine on either side, the diasteme may in fact be longer. It cannot possibly be shorter. This is a very conspicuous diagnostic feature of this new genus and species.'

On the right side the maxilla is broken posterior to the level of the canine. The distance between the mesial edge of the first molariform tooth to the edge of this break measures approximately 10,5 mm; and the distance between the mesial edge of the anterior 'conical' socket and the break measures some 7,0 mm. The distance between the mesial face of the first molariform tooth and the mesial edge of the first 'conical' socket measures about 3,5 mm.

As noted previously, the left canine socket and the damaged root which it contains have been exposed. The distance on this side between the mesial face of the first molariform tooth and the distal edge of the canine socket measures some 14,5 mm. The sockets of the left conical teeth have been damaged, but if one allows that the combined mesiodistal dimension of these teeth was the same as on the opposite side, then 3,5 mm may be subtracted from the above figure of 14,5 mm. The result is that the diastema separating the canine from the first conical tooth is closer to 11,0 mm than 14,0 mm; the distance between the first molariform tooth and the canine is about 14,0 mm.

In the earlier illustration of this specimen (Fig. 2 herein) the length of the diastema that is shown is 3,5 mm (Brink 1979: 44); the figure is reduced by half from actual size, and if the distance depicted is multiplied by two, the resultant length of the diastema is only 7,0 mm.

A diastema of some 11,0 mm (as determined by the present author) is not 'unusually extensive', in fact, neither is one of 14,0 mm for a *Diademodon* cranium of similar size.

Replacement of alisphenoid by the quadrate ramus of the pterygoid

Brink (1965: 105) noted that in the type of *Cragievarus kitchingi* 'the alisphenoid of the right side is exposed over its dorsal region and would appear to be typically diademodontid. Below, it definitely interferes with the pterygoid extension to the quadrate, but it seems as if it does not reach as far laterally.'

He also noted that, 'although there is clear interference on the part of the alisphenoids farther back, it would appear that the pterygoids themselves still reach the quadrates, as is characteristic of *Protacmon*'.

In a later paper it was noted that, 'from a very poor specimen it is interpreted in the illustrations that the pterygoids reach back to the quadrates, in which case *Cragievarus* is well separated from *Diademodon*. Watson (1920) created the genus *Protacmon* on the strength of a similar interpretation, and this is now regarded as a misinterpretation, and this may apply also to *Cragievarus*' (Brink 1979: 7).

The quadrate processes, whether they are formed by the alisphenoids or the pterygoids, are very poorly preserved. Both are distorted, they are covered with numerous cracks and a considerable amount of surface bone has been lost. Because of these factors the presence of a definite pterygo-alisphenoid suture could not be located. By the same token, the presence of this suture cannot be ruled out. The bone of this region is too poorly preserved to permit a definite confirmation or refutation of the earlier claim (Brink 1965), which Brink (1979: 7) later noted may be a misinterpretation.

Divergence of the quadrate rami of the pterygoid

In the original description (Brink 1965) it was noted that the quadrate rami of the pterygoid begin to diverge posterolaterally farther forward in *Cragievarus kitchingi* than is typical of *Diademodon*. This feature was added to the re-diagnosis of the former taxon (Brink 1979: 7).

The level at which the quadrate processes diverge is variable in *Diademodon*, and it appears to be related, to a certain extent, to cranial size. Even in crania of similar size there seems to be a certain amount of individual variation. Some idea of the amount of variation may be gained from an examination of Brink's (1979) illustrations of different *Diademodon* crania.

The outlines of the quadrate rami of *Cragievarus kitchingi* and four *Diademodon* specimens of similar size are presented in Figure 11. These outlines are adapted from Brink's (1979) drawings of the specimens and they serve to indicate the type of variation encountered.

Whilst the quadrate rami of *Cragievarus kitchingi* diverge somewhat further forward than in some *Diademodon* specimens (e.g. Fig. 11A–B) their level of divergence is comparable to that shown by other *Diademodon* specimens (e.g. Fig. 11C–D).

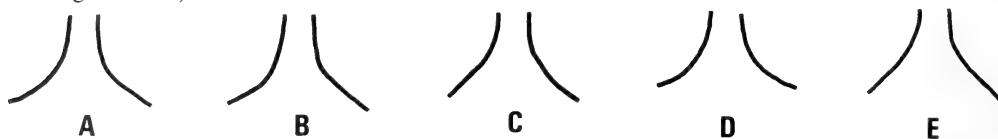


Fig. 11. Schematic outlines of diademodontine cranial bases to show the variation in the level of divergence of the quadrate rami. Specimens of similar cranial size. A–D. *Diademodon*. E. *Cragievarus*. A. Munich 1934 VIII 18. B. BPI.FN. 3769. C. BPI.FN. 3773. D. Camb. T. 462. All modified from Brink (1979). See text for explanation.

DISCUSSION

Cragievarus kitchingi was erected on the basis of an incomplete and poorly preserved skull of a gomphodont cynodont. In their taxonomic revision of the cynodonts, Hopson & Kitching (1972) proposed that *Cragievarus kitchingi* is a junior synonym of *Diademodon tetragonus*. Because of its incompleteness, the type of *Cragievarus kitchingi* was not included in the biometrical analyses of diademodontine crania (Grine & Hahn 1978; Grine, Hahn & Gow 1978; Bradu & Grine 1979). Recently, Brink (1979) has 'reinstated' *Cragievarus kitchingi* as a valid taxon within the Diademodontinae.

An examination of the type of *Cragievarus kitchingi*—no other specimen has been referred to this taxon (Brink 1979)—has revealed that most of its supposed diagnostic features are based upon (i) hypothetical plaster reconstruction (e.g. the lack of the jugal flange and the slight curvature of the temporal arch), (ii) the misinterpretation of damage for 'true' anatomical features (e.g. the forward height of the mid-sagittal crest and the foreshortened postero-inferior margin of the temporal arch), (iii) inaccurate plaster reconstruction (e.g. the powerful expansion of the ascending ramus of the dentary), (iv) incomplete preparation (e.g. the lack or supposed disposition of the post-temporal foramen, the lack of mandibular conical teeth and the length of the maxillary diastema), and (v) the obliteration of features by plaster (e.g. the lack of posterior sectorial teeth).

Other supposedly diagnostic characters (e.g. the relative width of the braincase and the level at which the quadrate rami diverge) have been shown here to be invalid when the size of the type specimen and the degree of variability of these features in *Diademodon* are considered. Another supposedly diagnostic feature of *Cragievarus kitchingi*, the replacement of the alisphenoid by the quadrate ramus of the pterygoid, can be neither substantiated nor refuted because of the poor preservation of the region. The validity of this last character has been questioned also by Brink (1979).

Furthermore, it has been shown upon removal of the plaster and further preparation that the specimen evinces no morphology by which it can be distinguished from *Diademodon*.

This specimen was recovered from the same fossil 'pocket' that yielded a number of *Diademodon* crania (Brink 1963; Kitching 1963). Kitching (1977) has stated that he believes these closely associated diademodontine specimens to be conspecific, and that the type of *Cragievarus kitchingi* represents a 'distorted growth stage' of *Diademodon tetragonus*. It is perhaps significant that whilst there are well over 100 available diademodontine skulls, crania, and mandibles from the South African *Cynognathus* Zone (= *Diademodon*–*Kannemeyeria* Assemblage Zone), neither Brink (1979) nor any other worker has been able to assign any of these remains, other than the holotype, to *Cragievarus kitchingi*.

CONCLUSIONS

The supposed diagnostic features of *Cragievarus kitchingi*, as preserved on the type and only specimen of this taxon, have been re-examined and shown to be invalid. The type displays no morphology by which it can be distinguished from *Diademodon*. As a result, the name *Cragievarus kitchingi* Brink, 1965, is considered to be a subjective junior synonym of *Diademodon tetragonus* Seeley, 1894.

Kitching's (1977) proposal that this specimen is a 'juvenile' individual of *Diademodon tetragonus* is supported.

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I thank the generous offices of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand, Johannesburg, for permission to prepare and describe the specimen. I thank various colleagues for reading and constructively criticizing this paper.

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Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

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SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

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DIADEMODON TETRAGONUS SEELEY, 1894
(REPTILIA, THERAPSIDA)

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(continued inside back cover)

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A NEW COMPOSITE JUVENILE SPECIMEN OF
AUSTRALOPITHECUS AFRICANUS
(MAMMALIA, PRIMATES) FROM MEMBER 4
STERKFONTein FORMATION, TRANSVAAL

By

F. E. GRINE

Cape Town Kaapstad

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A NEW COMPOSITE JUVENILE SPECIMEN OF *AUSTRALOPITHECUS AFRICANUS* (MAMMALIA, PRIMATES) FROM MEMBER 4, STERKFORTEIN FORMATION, TRANSVAAL

By

F. E. GRINE

South African Museum, Cape Town

(With 14 figures)

[MS. accepted 11 December 1980]

ABSTRACT

Two maxillae from the Sterkfontein fossil hominid site have been prepared. The left (Sts 70) and right (Sts 69) maxillae belong to a single juvenile individual. They occlude with the previously described 'gracile' australopithecine mandible (Sts 24). It is proposed that these three specimens, which are described here in detail, comprise a single juvenile individual. This composite specimen represents the most complete maxilla and occluding set of deciduous teeth of a juvenile australopithecine from South Africa, with the exception of the holotype of *Australopithecus africanus* Dart, 1925.

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INTRODUCTION

On 17 August 1936, Robert Broom recovered the first remains of an adult australopithecine at Sterkfontein (Broom 1936*a*, 1936*b*). Since then, excavations by Broom and Robinson over the periods 1936–1939 and 1947–1949, by Brain in 1956, by Robinson over 1957 and 1958, and by Tobias and Hughes from 1966 to the present have recovered a large number of remains of the 'gracile' australo-

pithechine, *Australopithecus africanus*, from the fossiliferous deposits of Sterkfontein. To date, the australopithecine fossils have derived solely from the lower breccia of the type site (Robinson 1952), or Member 4 sediments (Partridge 1978).

Although there are a relatively large number of adult australopithecine remains from Sterkfontein, the jaws and deciduous teeth of only eleven immature individuals have been recovered. Eight of these were found by Broom and Robinson and are housed in the collection of the Transvaal Museum (Sts 2, Sts 18, Sts 24, Sts 50/TM 1516, Sts 56, Sts 59, Sts 62 and Sts 67), the remaining three were discovered by Hughes and these are housed in the Department of Anatomy, University of the Witwatersrand Medical School (Stw 59, Stw 62 and Stw 67). None of these specimens consists of both mandibular and maxillary dentitions.

Recent work by the author on the Sterkfontein hominids revealed two specimens in the Transvaal Museum (Sts 69 and Sts 70) which required preparation and reconstruction. When cleaned, the two were found to represent the left and right maxillae and dentitions of a single juvenile individual together with the mandible and dentition of Sts 24. Together, these three specimens constitute the most complete occluding set of deciduous teeth of a single early hominid individual from South Africa, with the exception of the holotype of *A. africanus* from Taung.

The purpose of this paper is to describe in detail the gnathic parts and the dentition presented by the composite specimen, Sts 24/69/70. A comparative study of the dental morphology of this specimen will be presented in a future publication dealing with the dentitions of the South African australopithecines (Grine in prep.).

MATERIAL AND DESCRIPTIONS

SPECIMEN STS 69

This specimen was recovered from the Member 4 breccia in 1949 by J. T. Robinson. The description on the catalogue card reads: 'Fragmentary maxilla containing some teeth; 3 pieces.'

Prior to cleaning and reconstruction, the specimen consisted of three separate pieces of breccia with cross-sections of parts of the maxillary dentition exposed (Fig. 1). It was found that the three pieces fit together comfortably. After they were joined and the surrounding matrix was cleaned away, a reasonably well-preserved right maxilla with the dm^1 , dm^2 and M^1 was exposed (Fig. 2). Also partially exposed are the crowns of the developing M^2 and C ; small parts of the P^3 and P^4 are visible.

Maxilla (Figs 2–3)

The right maxilla is preserved from a point just behind the lateral wall of the socket of the di^2 anteriorly. Most of the lateral surface is intact, including much of the zygomatic process. The posterior surface of the maxillary tuberosity

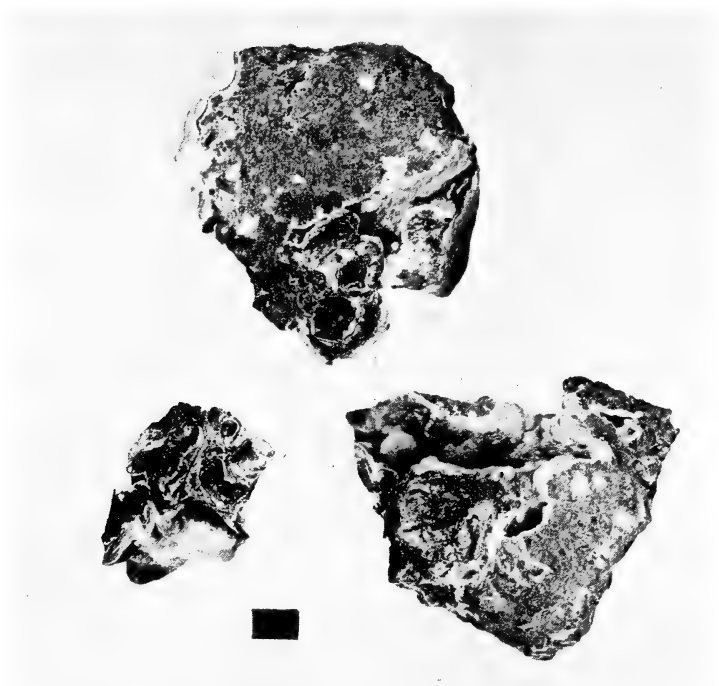


Fig. 1. Sts 69 prior to preparation and reconstruction. All three pieces of breccia contain fragments of dentition and maxillary bone. Scale in cm.

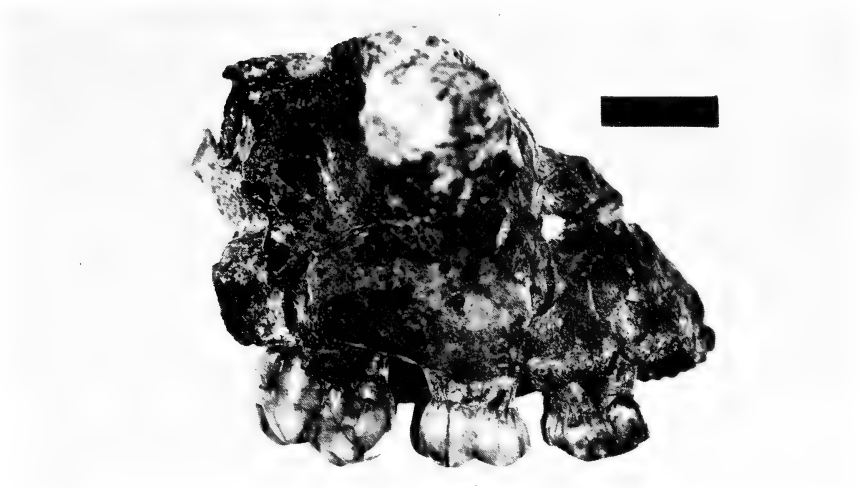


Fig. 2. Lateral view of Sts 69 after preparation. Note alveolar resorption and the separation of the tooth crowns. Scale in cm.

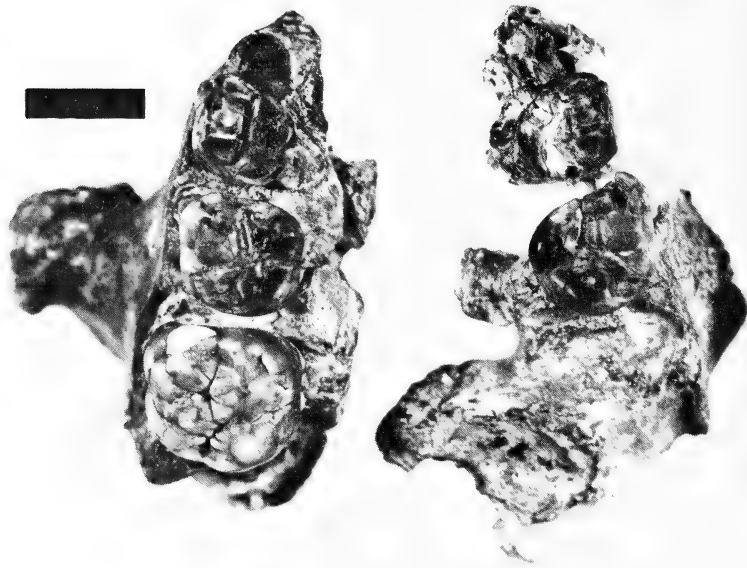


Fig. 3. Occlusal view of Sts 69 (left) and Sts 70 (right) in approximate anatomical alignment. Scale in cm.

is preserved superiorly, but inferiorly the bone has been broken away. Several pieces of bone have been lost from the lateral surface above the dm^1 , and a part of the buccal surface of the P^3 germ is visible in one of these areas. The zygomatic process is broken away laterally so that the zygomatic bone is not present, and the exposed end of this process has been crushed slightly with a large piece of the anterior face displaced forwards. A large piece of bone has been lost from the lateral surface over the distobuccal root of the M^1 . The medial, or internal surface has been severely damaged, and only a very small part of the horizontal process of the maxilla remains. Small, isolated parts of the lingual surface of the alveolar process remain intact. The crypts of the unerupted central and lateral permanent incisors are partially preserved. Part of the permanent canine germ and portions of the lingual surfaces of the premolar germs are exposed lingually. The matrix-filled socket of the d^c is preserved intact, and posteriorly a small part of the occlusal surface of the developing M^2 is visible. The dm^1 , dm^2 , and M^1 are well preserved. Diagenetic pressures have distorted the alveolar process slightly, so that the crowns of the deciduous and first permanent molars have been separated somewhat. Interproximal contact facets are present between these molars, but, as preserved, the crowns of the dm^1 and dm^2 are separated by about 1,3 mm and the crowns of the dm^2 and M^1 by some 1,5 mm.

Viewed from the lateral aspect, the alveolar margin is very slightly convex downwards anteroposteriorly. The margin appears to have undergone some resorption as portions of the buccal roots of the deciduous molars are visible.

The anterior surface of the zygomatic process arises at a level coincident with the mesiobuccal root of dm^2 . The lowest point of the root of the process arises above the distal edge of the dm^2 crown some 5 or 6 mm superior to the alveolar margin. The anterior surface of the zygomatic process slopes posterolaterally and it is gently concave medio-laterally. Its posterior surface slopes anterolaterally, but at its preserved lateral extent this face turns sharply posteriorly. The inferior surface of the zygomatic process slopes superiorly and laterally so that this face projects inferolaterally; it follows a broad, gentle curve so that no inframalar notch is present. The root of the zygomatic process is moderately robust.

The infraorbital foramen is situated at the junction of the zygomatic process and the lateral surface of the maxilla some 18,5 mm superior to the alveolar margin at the level of the mesiobuccal root of the dm^2 . Anterior to, and slightly below the infraorbital foramen the lateral surface of the maxilla shows a faint, nearly vertical bony ridge. This elevation descends on to the slight bulge formed by the developing P^3 crown. This ridge and the anterior surface of the zygomatic process define respectively the anterior and posterior boundaries of the shallow canine fossa, which is continuous with the sulcus below the infraorbital foramen. The canine jugum is weak.

Viewed inferiorly, the lateral surface of the maxilla curves gently forward and medially from the mesiobuccal root of the dm^1 . The anterior wall of the d^C socket is separated from the distal wall of the di^2 socket by some 3,3 mm of bone. It is evident that the deciduous incisors were situated at a level anterior to the d^C . The external surface of the maxilla courses anteromedially from the canine socket towards the incisal region. Thus, the lateral alveolar surface follows an even, and smoothly rounded contour from the dm^1 to the incisor sockets.

Deciduous dentition (Figs 2-3).

Maxillary first deciduous molar

The dm^1 is well preserved. The crown is very nearly complete, with some enamel loss to its lingual surface and a number of fine cracks covering the lingual half of the occlusal surface.

Viewed occlusally, the crown is square in outline; this arrangement is disturbed slightly by the presence of a prominent swelling over the mesiobuccal aspect of the crown. Although the lingual half of the occlusal surface has been reduced to a large dentine basin, it is apparent from the symmetry of the crown that all four principal cusps were present and it seems that all were well developed. The protocone is judged to have been the largest cusp. The paracone is larger than the metacone. The relative size of the hypocone cannot be ascertained.

Occlusal wear is heavy. The entire lingual half of the crown has been reduced to a large, buccolingually concave dentine basin. The mesial, distal, and lingual sides of this exposure are bordered by a thin enamel rim. The dentine exposure is demarcated buccally by a relatively straight longitudinal line which transects the paracone and metacone. The paracone and metacone are worn so that no buccal demarcation between them is visible. Two rather distinct planes of wear are presented on the buccal side of the occlusal surface; these planes are separated along the main crest of the metacone. The mesial plane is the larger, and it slopes mesiolingually from the metacone across the paracone. The distal plane slopes rather strongly distolingually from the metacone across the distal marginal ridge. A small circular patch of dentine is exposed on the tip of the paracone and a smaller pit is exposed on the tip of the metacone.

Interproximal attrition appears to have been moderate mesially with the d^c , and slight to moderate distally with the dm^2 . A broad (2,3 mm buccolingual; 1,7 mm high), concave, contact facet is present on the mesial surface. The facet is more strongly concave at its buccal extent, and it is situated over the upper half of the face (as preserved); its lingual border is situated approximately in the middle of the mesial surface. The mesial facet thus extends over the buccal part of this face. The distal surface presents a broad (3,9 mm buccolingual), flattened and rectangular-shaped facet. This facet is situated slightly more towards the lingual than the buccal side of the distal surface.

Occlusally, it is apparent that a small to moderate sized mesiostyle (=parastyle) was present mesial to the paracone. A shallow, narrow groove separates the paracone from remnants of the mesiostyle occlusally. The mesial marginal ridge is moderately thick and it courses on to the summit of the mesiostyle. The fovea anterior is represented by a relatively shallow, wedge-shaped transverse groove; it is broader buccally but narrows lingually to a thin groove where it ends approximately one-third of the way across the crown. The fovea is enclosed distally by the main crest of the paracone. It appears that a small distostyle (=metastyle) was present distal to the metacone. This region is worn, however, and the only indication of this accessory cuspule is a slight swelling of the buccal surface at the distal extremity of the crown. The distal marginal ridge, though worn, appears to have been somewhat thicker than the mesial marginal ridge; it is continuous up on to the distostyle. The buccal end of the fovea posterior, or talon basin, is represented by a narrow transverse groove.

Because of wear and damage there is no trace of the lingual developmental groove, if one were present originally. Also, the region of the mesiolingual face of the protocone where the Carabelli trait is usually expressed has been obliterated by wear.

The buccal surface is rather vertical, with a slight cervical enamel prominence present at the base of the metacone. The cervical enamel line extends considerably further over the mesiobuccal root than over the distobuccal root. The cervical enamel prominence above the paracone is extremely well de-

veloped, such that a rather large *tuberculum molare* is presented. The *tuberculum molare* projects both cervically and laterally as a bulbous swelling. A moderately thick crest of enamel courses vertically from the mesiostyle occlusally to blend into the lower part of the mesial end of the *tuberculum molare*. This crest is demarcated behind by a moderately deep, broad, vertical groove running from between the paracone and mesiostyle to the *tuberculum molare*. The distal half of the buccal surface possesses a large, moderately deep, V-shaped depression. The anterior border of this depression runs distocervically from just behind the tip of the paracone to a point some 2,3 mm from the cervical margin over the distobuccal root. The posterior border courses from this point to a level just distal to the tip of the metacone. The floor of this depression is flat.

The principal dimensions of the crown are as follows:

	MD diameter (as measured)	BL diameter (as measured)	BL diameter (incl. <i>tuberculum molare</i>)
Rdm ¹	8,5 mm	9,2 mm	9,6 mm

The radicular system comprises three separate roots—two buccal and one lingual. The buccal root neck is extremely low. The buccal roots are mesiodistally compressed, the mesiodistal diameters at the cervical margin being 2,9 mm and 2,6 mm for the mesiobuccal and distobuccal roots respectively. They are buccolingually elongate. The two roots diverge at a considerable angle (approximately 45°). The lingual root appears to be the most robust and it courses strongly lingually away from the crown.

Maxillary second deciduous molar

The right dm² is complete and well preserved. Part of the lingual root together with the adjacent alveolar bone has been broken away. A thin, calcite-filled crack runs vertically from the cervical margin across the lingual surface between the protocone and hypocone, and continues over on to the occlusal surface, in the same plane, across about half of the crown.

Viewed occlusally, the crown is very nearly square in outline. The distal border is slightly convex buccolingually. All four principal cusps are present and well developed. The protocone is the largest cusp by a considerable margin. The paracone, metacone and hypocone are nearly equal in size.

Occlusal wear is moderate. Wear is heavier lingually, with the protocone and hypocone considerably reduced in height relative to the paracone and metacone. The protocone has suffered the heaviest wear. A large, mesiodistally elongate and buccolingually concave dentine exposure is present on the tip of this cusp. The lingual side of the protocone bears two bevelled enamel facets separated along a transverse crest. The anterior facet slopes sharply mesiolingually and the posterior facet slopes sharply distolingually. The hypocone shows a large, slightly convex enamel facet that slopes mesiolingually. A moderately large, circular and concave area of dentine is exposed near the tip of this cusp. The paracone is slightly worn with an enamel facet on the mesiolingual slope of this cusp. The metacone is the least worn of all the cusps, and it shows only faint

enamel wear. Like the dm^1 , this tooth displays considerable disparity in the degree of occlusal wear between the buccal and lingual sides of the crown.

Mesial interproximal contact is judged to have been slight to perhaps moderate in degree; a moderately large, flattened rectangular facet is present in the middle of this face. Contact distally with the M^1 appears to have been very slight—the mesial surface of the latter tooth possesses a moderate-sized, circular and faintly attrited facet.

Occlusally, there is no evidence of the presence of any accessory cuspules. The mesial marginal ridge has been slightly damaged adjacent to the occlusal border midway along the mesial face. It is worn, but appears to have been moderately thick. There is no trace of a fovea anterior. The distal trigon crest (=crista obliqua) is moderately well developed. It is rather thick and, though worn, it appears to have been continuous between the protocone and metacone. The distal marginal ridge is moderately thick but very low. It is thicker and higher lingually, where it arises from the distobuccal aspect of the hypocone. The ridge slopes cervically and becomes progressively thinner and lower as it proceeds buccally. The distal marginal ridge is at its lowest where it meets the distal surface of the base of the metacone, and at this point it is more shelf-like than ridge-like in form. The fovea posterior, or talon basin, is represented by a moderately deep but narrow and short transverse groove. It is restricted to the buccal half of the crown, and it drains distobuccally behind the metacone. At the base of the hypocone the lingual end of the groove turns sharply mesially where it continues between the metacone and hypocone. Although the lingual groove has been obliterated by wear, it is judged to have been continuous with the mesial limb of the fovea posterior.

The height of the lingual surface has been considerably reduced by wear. It is slightly convex occlusocervically with a faint cervical enamel prominence present. The mesiolingual surface of the protocone has been worn beyond the level at which the Carabelli trait is usually expressed, and, therefore, the presence or absence of this feature cannot be ascertained.

The buccal surface is rather flat and vertical occlusocervically; only a very slight cervical enamel prominence is present. The cervical line is horizontal. The buccal groove is represented by a short, rather narrow cleft. This surface presents no evidence of hypoplastic or perikymatous enamel.

The principal dimensions of the crown are as follows:

	MD diameter (as measured)	BL diameter (as measured)
Rdm ²	10,3 mm	10,8 mm

The radicular system consists of three separate roots—two buccal and one lingual—arranged very similarly to the roots of the dm^1 . The root neck is very low buccally. The lingual root appears to have followed a somewhat more vertical course than its counterpart on the dm^1 . The mesiodistal dimensions of the mesiobuccal and distobuccal roots at the cervical margin are 3,1 mm and 2,9 mm respectively.

Permanent dentition (Figs 2–3)*Maxillary first permanent molar*

The crown and roots of the right M^1 are preserved. The crown is relatively complete and well preserved. Large chips of enamel have been broken away from the buccal side of the mesial face and from the cervical region of the distolingual corner. The buccal surface has suffered some slight cracking.

Viewed occlusally, the crown is square in outline. All four principal cusps are present and well developed. The protocone is the largest cusp by a considerable margin. The paracone is slightly larger than the metacone, the latter being nearly equal in size to the hypocone.

Occlusal wear is very mild. The protocone and the hypocone show faint enamel faceting; on the former this is restricted to the distal and distolingual sides of the cusp, whilst the hypocone shows a small facet on its apex. The mesial surface shows a moderate-sized, very lightly attrited interproximal contact facet. It is evident that this tooth had reached partial occlusal contact just prior to the time of death.

Although the mesiobuccal corner has been damaged, it appears that no mesiostyle was present. There is no development of accessory cuspules on the crown. The mesial marginal ridge is moderately thick but low, and it is incised in its middle by a shallow, broad groove. The fovea anterior is represented by a moderately deep, rather broad transverse groove situated symmetrically in the middle of the mesial part of the crown. It is bounded behind by a thick and high transverse crest formed by ridges from the paracone and protocone. This crest is much higher than the mesial marginal ridge. The ridges that form the transverse crest are separated by a very narrow groove—the crest from the paracone is slightly longer than that from the protocone. The trigon basin is deep and wide, and the sides of the cusps slope gently towards the bottom of the basin. The distal trigon crest is of moderate height and thickness. A shallow, narrow groove courses over its summit. The form of the distal marginal ridge resembles that shown by the dm^2 . It is moderately thick but low, and it is continuous on to the distobuccal aspect of the hypocone lingually, but as the ridge courses buccally it becomes lower. It reaches only the bottom of the distal side of the metacone. The talon basin is represented by a relatively deep and broad transverse groove which is continuous with the groove separating the hypocone and metacone and the hypocone and protocone.

The lingual surface is slightly convex occlusocervically, especially over the cervical third of its height, and a moderately developed cervical enamel prominence is present. The lingual groove is deep, but it is rather narrow over the cervical portion of its length. It courses vertically for about two-thirds of the crown height where it ends abruptly. The mesiolingual and lingual aspects of the protocone display a series of grooves and enamel protuberances that represent the Carabelli trait. The mesiolingual aspect of the protocone presents a relatively deep, 2 mm long, horizontal groove which is bounded by a thin enamel ridge.

The ridge is incised by a narrow groove. There is a disparity between the planes occupied by the surface of the protocone above and the mesiolingual surface of the crown below this horizontal groove. A second groove is etched into the lingual surface; this groove, which is obliquely orientated, courses distocervically to mesio-occlusally, is some 1,8 mm long, and at its uppermost end it is separated from the distal end of the horizontal groove by about 1,5 mm of enamel. The surface of the crown cervical of this series of grooves is somewhat more expanded than the surface of the protocone above the groove.

The buccal surface is nearly flat and vertical occlusocervically. There is no indication of a cervical enamel prominence on this face. The buccal groove is very shallow and rather narrow; it extends vertically over about three-quarters of the crown height. There is no evidence of hypoplastic or perikymatous enamel on any of the crown surfaces.

The radicular system is obscured for the most part, but it appears to consist of three separate roots. The lingual root displays a marked longitudinal groove in its middle; this root may comprise two separate canals.

The principal dimensions of the crown are as follows:

	MD diameter (as measured)	BL diameter (as measured)
RM ¹	13.1 mm	13.8 mm

SPECIMEN STS 70

This specimen was discovered by J. T. Robinson in the Member 4 breccia in 1949. The description on the catalogue card reads: 'Incomplete and crushed maxilla containing some of the milk dentition and well-formed but unerupted anterior permanent teeth.'

Prior to cleaning and reconstruction, the specimen consisted of three separate pieces of breccia containing parts of a poorly preserved maxilla and deciduous dentition (Fig. 4). The permanent central and lateral incisors were found in a separate box in the collection which was labelled as containing



Fig. 4. Sts 70 prior to preparation and reconstruction. Scale in cm.

unidentified bone fragments. It was discovered that one of the pieces of breccia contained half of the crown of a right permanent maxillary canine and this fitted perfectly on to part of the RC crown contained in the maxilla of Sts 69. However, this did not provide unequivocal evidence for the association of Sts 69 and Sts 70 because the piece might have been placed erroneously in the box containing the Sts 70 specimen. One of the pieces of breccia contained the buccal half of the crown of the Ldm¹; this was removed and fitted to the remainder of the tooth. The medial surface of the maxilla fragment was very badly eroded, and it was decided to sacrifice this part of the bone in order to extract the crowns of the developing LP³ and LP⁴.

Final preparation revealed a very badly fragmented and incomplete left maxilla containing the damaged Ld^c, Ldm¹ and Ldm² (Fig. 3).

Maxilla (Fig. 3)

The bone is very incomplete and comprises two pieces. The anterior of the two consists of a small piece of the anterolateral surface above the root of the deciduous canine, a small part of the lingual alveolar surface anterior to the dm¹ and medial to the d^c. This piece contains part of the crypt for the developing I¹ and a portion of the distal alveolar wall of the di² root. The larger piece shows the inferior root of the zygomatic process; it is broken anteriorly vertically above the middle of the dm² and it ends posteriorly opposite the alveolus of the distobuccal root of the M¹. A moderately large piece of what appears to be the horizontal palatal process of the maxilla is attached to the posterior piece of the maxilla by a bridge of breccia. The maxilla is too incomplete to warrant an anatomical description.

Deciduous dentition (Fig. 3)

Maxillary deciduous canine

A small part of the crown and the broken, exposed root of the left d^c are present. The crown consists only of the distolingual cervical corner. The occlusal aspect of the preserved portion of the crown is worn with a rather strong distolingual bevel; the most distal part shows a dentine exposure.

The root is single and straight. It is evident that the root had a compressed ovoid outline in cross-section, with the broadest axis mesiodistal. The buccal surface possesses a slight vertical groove.

It is not possible to obtain measurements of either the crown or the root.

Maxillary first deciduous molar

The damaged, incomplete crown and part of the radicular system of the left dm¹ are preserved. A large section of the lingual part of the occlusal surface and both the mesial and distal crown surfaces are damaged and/or missing. The lingual root remains intact but the two buccal radiculæ are missing.

The degree, extent and the finer details of occlusal wear are identical to those shown by the Rdm¹ of Sts 69. The occlusal morphology of this crown, as

preserved, is identical to that displayed by the homologous tooth of Sts 69. Buccally, the *tuberculum molare* appears to be slightly more swollen and accentuated than that on the dm^1 of Sts 69, and the V-shaped depression on the buccal surface is somewhat smaller here than on the other tooth. The lingual root is similar in size and orientation to that of Sts 69.

The principal dimensions of the crown are as follows:

	MD diameter (as measured)	BL diameter (as measured)	BL diameter (incl. <i>tuberculum molare</i>)
Ldm ¹	8,6 mm	9,0 mm	9,3 mm

Maxillary second deciduous molar

The damaged, incomplete crown and the severely damaged radicular system of the left dm^2 are present.

The buccal side of the mesial surface as well the occlusal surface of the paracone have suffered slight enamel loss. A relatively wide crack runs obliquely across the metacone on to the distobuccal corner with some slight displacement of the adjacent enamel. Another crack runs across the protocone, hypocone and the distolingual corner of the crown. This crack is narrow but some enamel has been lost from along its borders.

The degree, extent and finer details of occlusal wear shown by this tooth are identical to those evinced by the Rdm^2 of Sts 69. Also, the morphological details of the occlusal, buccal and lingual surfaces are essentially mirrored by the dm^2 of Sts 69.

The principal dimensions of the crown are estimated as follows:

	MD diameter (estimated)	BL diameter (estimated)
Ldm ²	10,2 mm	11,2 mm

Permanent dentition (Fig. 5)

Maxillary central permanent incisor

The isolated crowns of both the left and right I^1 's are present. The crown of the left tooth is the more complete of the two. The mesial and distal halves of the LI^1 crown have been displaced slightly along a straight vertical crack through the middle of the tooth. The mesial half of the lingual cervical margin has suffered from loss of enamel. The root is only partially developed on the mesial and distal aspects of the crown. The right crown has been broken along an irregular, oblique plane from the middle of the buccal surface to the cervical margin of the lingual surface. The mesial side of the remaining part of the crown is separated slightly from the rest of the tooth by a slightly curved vertical crack.

The mesial corner of the incisal edge is rather sharply angulated, whilst the distal one is more smoothly curved. The incisal edge of the right crown has a single, small mammelon in its middle with the edges mesial and distal to it flat and horizontal. The lingual aspect of this edge shows several very faint vertical grooves. The incisal edge of the left crown, however, shows some four small mammelons from the mesial edge to the middle; the distal half of this edge is rather flat and horizontal in disposition.



Fig. 5. Permanent dentition associated with Sts 70. Scale in cm.

The labial surface is slightly convex incisocervically over its incisal half; the cervical portion is rather flat and vertically inclined. There is no cervical enamel prominence present. A number of faint, irregular vertical grooves cover most of the labial surface. Viewed from the labial aspect, the crown is nearly rectangular in outline. Its height is greater than its mesiodistal diameter. The cervical region is only slightly tapered, so that the mesiodistal diameter at the incisal margin is just slightly greater than that cervically.

Lingually, the mesial marginal ridge is faintly developed, and this only over the incisal third of the crown. The distal marginal ridge is slightly thicker and shows more relief than the mesial marginal ridge. Approximately at mid-crown height the distal marginal ridge blends imperceptibly into the basal or gingival swelling. This prominence is rather well developed, and although it is symmetrical, the distal portion is somewhat more swollen than the mesial end. Two central vertical ridges arise from the basal prominence. The mesial of these ridges is thin and low and the distal, which arises from the more swollen part of the basal prominence, is somewhat better developed and longer than the mesial. On the left crown the mesial of the two central ridges is represented by two, thin parallel crests; and the distal ridge is better developed than on the left tooth. The lingual surface is slightly concave mesiodistally and moderately concave incisocervically.

The principal dimensions of the crowns are as follows:

	MD diameter (as measured)	BL diameter (as measured)	Height (as measured)
LI ¹	10,0 mm	—	—
RI ¹	10,0 mm	8,5 mm	14,4 mm

Maxillary lateral permanent incisor

The isolated crowns of the left and right I²'s are present. The crown of the left tooth is well preserved and very nearly complete, but it has suffered some slight damage to the lingual cervical margin. A small piece of alveolar bone is attached to the base of the mesial surface of this crown. The right tooth is more damaged than the left. A small chip of enamel has been lost from the incisal edge and a large, wedge-shaped section of the crown has broken away from the lingual surface. The cervical enamel margin has been damaged round the entire periphery of the crown. A small piece of alveolar bone is attached to the base of the distal surface of this tooth. Neither tooth possesses any trace of the root.

The mesial end of the incisal edge is somewhat rounded, but it is considerably sharper in appearance than the distal end, which exhibits a long, gentle curvature. The incisal edge is notched slightly mesial to its middle, and the mesial portion is both shorter mesiodistally and higher than the distal part. A single, faint mammelon is developed at the distal end of the incisal notch.

The labial surface is only faintly convex incisocervically. Viewed from the labial aspect, the crown is somewhat rectangular in outline—its height exceeds its mesiodistal diameter. The cervical portion of the crown is slightly narrower mesiodistally than the incisal part. The labial surface displays several faint, irregular vertical grooves. Along the mesial border of this face, a faint vertical ridge courses incisally for most of the crown height from the cervical region.

Lingually, the mesial and distal marginal ridges are moderately well developed. They are narrow and low incisally, where they blend into the lingual surface some 2 or 3 mm short of the incisal edge. The ridges become progressively thicker and higher as they course cervically. The cervical swelling or prominence is damaged. The mesial and distal marginal ridges follow a convergent course cervically where they are separated by a relatively deep but narrow groove. It is not possible to determine whether these ridges remained separate up to the cervical line or whether they joined to form a single basal prominence. No median ridge development is present. The lingual surface is rather flat incisocervically and slightly concave mesiodistally.

The principal dimensions of the crowns are as follows:

	MD diameter (as measured)	BL diameter	Height (estimated)
LI ²	6,5 mm	—	10,0 mm
RI ²	6,9 mm	—	—

Maxillary anterior premolar

The isolated crown of the left P³ is present. The specimen is represented by an apparently incompletely developed crown with slight damage to parts of the cervical margin. Root development had not been initiated at the time of death. However, it is apparent that the crown was almost fully developed; perhaps some enamel would have been added to the buccal and lingual cervical margins.

Viewed from the occlusal aspect, the crown is ovorectangular in outline, with the buccal and lingual sides rounded and the buccolingual axis longer than

the mesiodistal. The two principal cusps are present. The buccal cusp is considerably larger than the lingual. The apex of the buccal cusp is situated approximately midway between the mesial and distal ends of the crown, the mesial slope of this cusp is sharp whilst its distal aspect is more inflated in appearance. The lingual cusp is lower and areally smaller than the buccal cusp, and it is situated mesial to the mid-crown transverse axis which bisects the buccal cusp. The shorter mesial part of the lingual cusp is rather sharp, and its distal aspect is thickened.

The mesial marginal ridge is extremely low. It is higher and slightly thicker lingually where it arises from the tip of the lingual cusp. It loses height as it courses buccally till it meets the base of the buccal cusp, where it is represented by a flat shelf. The fovea anterior is represented by a broad, flattened surface which is bounded posteriorly across its buccal half by a well-developed crest from the buccal cusp.

Two well-developed crests from the buccal cusp, and a single, moderately well-developed ridge from the lingual cusp are separated by a deep but narrow longitudinal groove which traverses the mid-crown longitudinal axis.

The distal marginal ridge is thick at its buccal and lingual extremes, but is low and relatively thin in its middle. Where the ridge joins the lingual cusp a short, thick crest courses buccally. Distal to the buccal cusp, the distal marginal ridge supports a short, mesiolingually directed crest. The fovea posterior, which is larger than the fovea anterior, is represented by a relatively deep basin.

The lingual surface is slightly convex occlusocervically, and it is well rounded mesiodistally.

The buccal surface is flat occlusocervically, the cervical portion being lateral to the occlusal part of this face. The mesial and distal aspects of the buccal face are indented by rather deep vertical grooves. The mesial groove is broader occlusally, and cervically it narrows to a relatively deep cleft; it ends abruptly just above the cervical enamel margin. The distal groove is longer than the mesial one, and it courses vertically from the posterior aspect of the buccal cusp to near the cervical margin. It is bounded behind by a prominent vertical enamel crest.

The principal dimensions of the crown are as follows:

	MD diameter (as measured)	BL diameter (as measured)
LP ³	9,1 mm	12,4 mm

Maxillary posterior premolar

The badly damaged and incomplete, immature crown of the left P⁴ is present. Only the occlusal portion of the buccal cusp and the mesio-occlusal part of the lingual cusp are present. The distolingual quadrant of the crown has been badly distorted and damaged. No trace of any radicular formation, if any were present at the time of death, is presented.

It is evident that the buccal cusp is considerably larger, both areally and in height, than the lingual cusp. The buccal cusp appears to be situated so that its

tip is coincident with the mid-crown transverse axis of the crown. The lingual cusp is situated mesial to the buccal cusp, in the mesiolingual quadrant of the crown. A moderate-sized, incompletely separate cuspsule occupies the mesial border of the buccal cusp. The mesial marginal ridge is like that of the P^3 in form; it rises high on to the lingual cusp but ends at the base of the buccal cusp (more particularly, at the base of the mesiobuccal cuspsule). The fovea anterior is represented only by a broad, flattened and buccally sloping shelf. It is bounded distally by crests from the buccal and lingual cusps. These crests are separated in the middle of the crown by a deep, narrow longitudinal groove.

The buccal surface, as preserved, presents the tip of what appears to have been a moderately well-developed mesial enamel ridge. The ridge arises occlusally as a relatively thin crest opposite the junction between the buccal cusp and the mesiostyle. After a short distance the crest broadens considerably; it is demarcated mesially by a V-shaped depression and distally by a moderately deep groove. There is no evidence of the presence of a distal buccal groove.

Because of damage, no measurement of the dimensions of this tooth can be recorded.

SPECIMENS STS 69/STS 70 COMPOSITE (Figs 3, 6-7)

The left and right maxillae, Sts 69 and Sts 70, and their associated teeth are considered to belong to the same individual for several reasons. Firstly, as mentioned above, the fragment of the permanent canine associated originally with Sts 70 was found to fit perfectly the RC crown contained in the Sts 69 maxilla. Secondly, there is very close correspondence of the morphological features of the dm^1 and dm^2 of the two specimens (Figs 3, 7), and the dimensions of these teeth are nearly identical. Thirdly, the degree, extent and details of the patterns of occlusal wear between the deciduous molars in the two maxillae are identical. Fourthly, the right permanent central and lateral incisors associated originally with Sts 70 fit snugly into the remnants of the corresponding crypts in Sts 69 (Fig. 6). More particularly, the small piece of alveolar bone attached to the RI^2 crown corresponds in size and outline to an area of bone

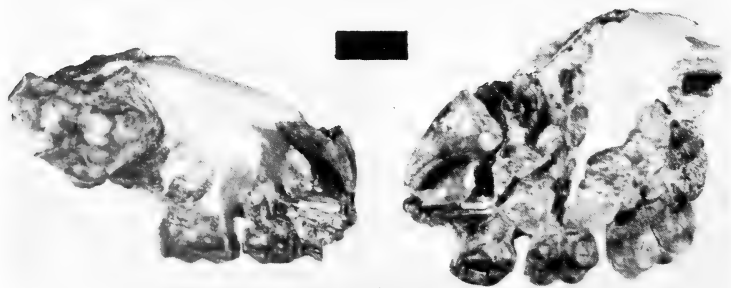


Fig. 6. Medial view of Sts 70 (left) and Sts 69 (right) with the permanent incisors placed in their crypts. Scale in cm.

that is missing from the lateral wall of the lateral permanent incisor crypt in the Sts 69 maxilla. Finally, the state of preservation and the coloration of the enamel of the deciduous molars (and permanent incisors) contained by the two specimens are very much alike.

The two reconstructed maxillae with the permanent incisors placed in their crypts are shown in Figure 7 in near anatomical position.

SPECIMEN STS 24

This specimen was recovered from the lower, or Member 4, breccia by Broom and Robinson on 11 March 1948. It consists of the badly damaged alveolar portion of a mandibular corpus with the left deciduous incisors, the left and right deciduous canines and first molars, the right second deciduous molar and the right first permanent molar (Fig. 8). Broom & Robinson (1950) extracted the developing crowns of the right permanent central incisor, the right and left lateral permanent incisors and the right anterior premolar from the mandible.

Additional preparation was performed on this specimen in order to expose the lingual aspects of the deciduous and permanent molars and the right mandibular corpus, and the alveolus of the Rd_c (Fig. 9). In addition, the crown of the LP_3 and the damaged, incomplete crown of the RP_4 were removed from the bottom of the mandible.

The deciduous and permanent teeth contained in this mandible have been briefly described and figured by Broom & Robinson (1950) and Robinson

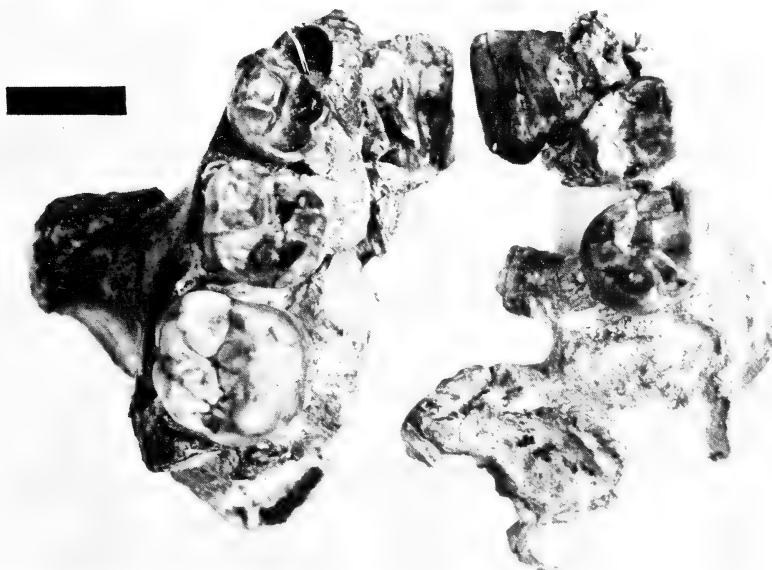


Fig. 7. Occlusal view of the Sts 69/Sts 70 composite with permanent incisors in their crypts. Arranged in approximate anatomical position. Specimen now catalogued as Sts 24a.
Scale in cm.

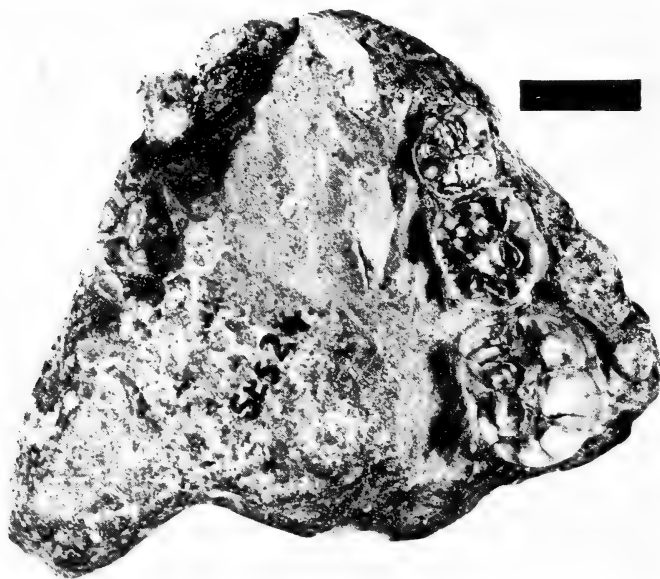


Fig. 8. Occlusal view of Sts 24 prior to further cleaning.
Scale in cm.

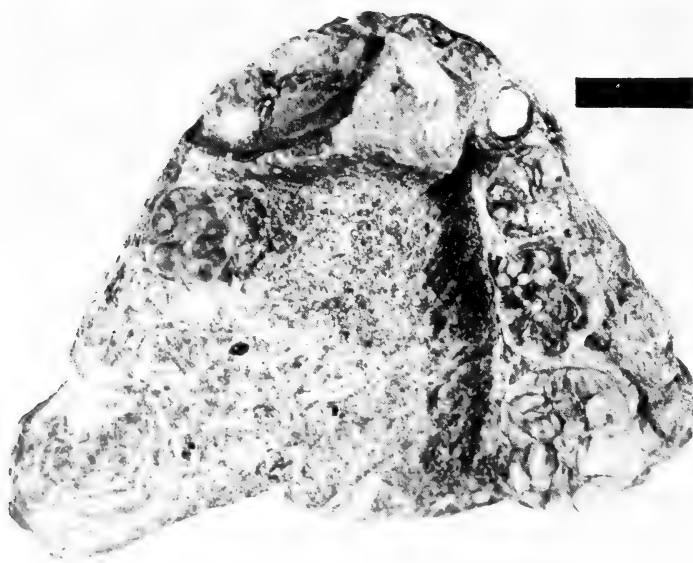


Fig. 9. Occlusal view of Sts 24 after further cleaning.
Scale in cm.

(1956). The following is a list of descriptive text pages and figures of these teeth in the aforementioned publications.

BROOM & ROBINSON (1950)

Descriptive text

<i>specimen</i>	<i>page</i>
Mandible	42
di ₁	50
di ₂	51
d _C	51
dm ₁	51-54
dm ₂	54-55
I ₁	42
I ₂	43
P ₃	43-45
M ₁	45

Illustrations

<i>specimen</i>	<i>figure</i>	<i>page</i>
di ₁ buccal view	15A	42
di ₂ buccal view	15B	42
d _C buccal view	15C	42
di ₁ -d _C anterolateral view	plate 3 (fig. 14)	
dm ₁ buccal view	15L	42
dm ₂ buccal view	15K	42
dm ₁ -M ₁ occlusal view	17C	50
dm ₁ -M ₁ occlusal view	plate 4 (fig. 18)	
I ₁ buccal view	15D	42
I ₁ lingual view	15E	42
I ₁ mesial view	15F	42
I ₂ buccal view	15G	42
I ₂ lingual view	15H	42
I ₂ distal view	15I	42
P ₃ buccal view	15M	42
P ₃ distal view	15N	42
P ₃ occlusal view	15O	42
M ₁ buccal view	15J	42

ROBINSON (1956)

Descriptive text

<i>specimen</i>	<i>page</i>
di ₁	130
di ₂	130
d _C	132-133
dm ₁	136-137
dm ₂	141-142
I ₁	36
I ₂	37-38
M ₁	104-106

Illustrations

<i>specimen</i>	<i>figure</i>	<i>page</i>
dm ₁ buccal view	39b	136
dm ₁ occlusal view	38b	135
I ₁ lingual view	10b	38
I ₂ lingual view	10c	38
M ₂ occlusal view	30b	105

Although these teeth have been described briefly and illustrated elsewhere, they will be described in detail and figured here for completeness.

*Deciduous dentition (Figs 9–12)**Mandibular central deciduous incisor*

The worn crown and intact root of the left di_1 are present. The lingual surface of the tooth is covered by matrix.

The incisal edge is moderately worn with a slight mesiolingual slope. This edge shows a large dentine exposure which is rimmed by a thin enamel wall. The height of the crown appears to have been reduced considerably by wear. The labial surface is very faintly convex incisocervically, there being no cervical enamel prominence at all. This surface is smooth, and the cervical portion of the crown appears to have been tapered so that the mesiodistal diameter of the incisal edge would have been greater than that at the incisal margin.

Broom & Robinson (1950) recorded the mesiodistal diameter of the extant crown as 4,1 mm; Robinson (1956) measured it as 4,2 mm and estimated that this dimension of the unworn crown would have been about 4,7 mm. The height of the crown was recorded as 4,0 mm by Broom & Robinson (1950) and as 3,4 mm by Robinson (1956). The dimensions of the crown, as recorded by the present author, are as follows:

	MD diameter (as measured)	MD diameter (est. original)	BL diameter	Height (as measured)	Height (est. original)
Ldi_1	4,2 mm	4,4 mm	—	3,7 mm	?

The root is elongate and appears rather large relative to the size of the crown. It courses straight downward for most of its length, with the apical third tapering and sloped slightly mesially. The root is some 20,8 mm long and it measures mesiodistally some 3,0 mm at the cervical margin.

Mandibular lateral deciduous incisor

The badly damaged crown and the complete root of the left di_2 are preserved. The Rdi_2 is represented only by a small part of the lingual enamel surface and a broken root which is embedded in its socket.

When cleaned originally, the crown of the left incisor was 'perfectly preserved except that the top of the crown is a little worn (Broom & Robinson 1950: 51). Later, Robinson (1956: 130) recorded that the 'crowns of the lateral incisors are too damaged for either measurement or description'.

At present, the crown of the Ldi_2 is missing a large chip of enamel from the mesiolabial aspect and the entire upper portion has been broken away along a plane that slopes steeply cervically from mesial to distal. The root is complete, but only the mesiolabial aspect is exposed.

Fortunately, the labial aspect of the complete crown was illustrated in a drawing by Broom & Robinson (1950, fig. 15B) and in a photograph (Broom & Robinson 1950, plate 3 (fig. 14)). It is evident from these figures that the crown had a somewhat rectangular outline, and it appears that wear was moderate. The incisal edge was somewhat convex, with a short mesially sloping part and a longer and more steeply sloping distal bevel. It is evident also that a faint to slightly developed enamel crest rose vertically from the cervical margin

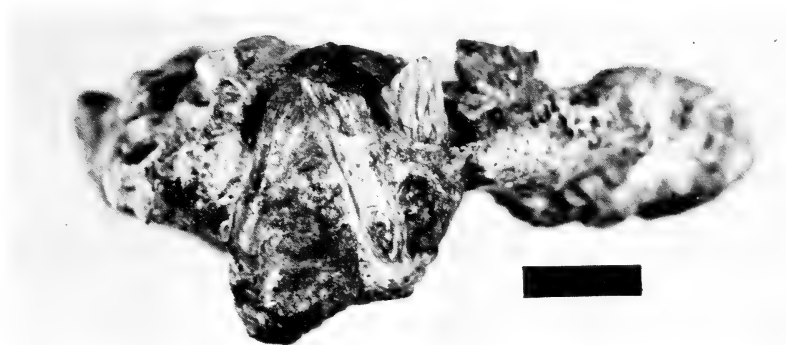


Fig. 10. Buccal view of deciduous incisors and canine of Sts 24. Scale in cm.

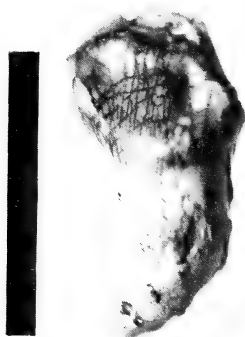


Fig. 11. Lingual view of Rd_C of Sts 24. Scale in cm.

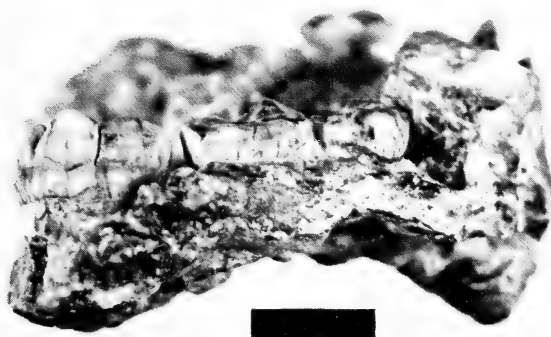


Fig. 12. Buccal view of right deciduous and first permanent molar of Sts 24. Scale in cm.



Fig. 13. Isolated permanent teeth of Sts 24. Scale in cm.

along the distal end of the labial face to the incisal edge. The buccal face is nearly flat and vertical incisocervically, and a cervical enamel prominence is not present.

The crown appears to have been considerably larger than that of the di_1 . Although no measurements can be recorded for the crown, Broom & Robinson (1950) determined the mesiodistal diameter as being 5,5 mm and the height (worn) as 6,7 mm. Because of damage, no measurements of the crown can be made now.

The root is moderately robust, elongate and straight. The length of the root measures some 11,2 mm, and its mesiodistal diameter at the cervical margin is approximately 3,5 mm.

Mandibular deciduous canine

Both the left and right deciduous canines are represented. The left d_c is represented by a damaged crown and the Rd_c consists of a damaged crown and root. The crown of the Ld_c is preserved in anatomical position, whilst the Rd_c has been dislodged from its alveolus—the crown and the upper half of the root are isolated, and the lower half of the root is attached by its lingual aspect to matrix.

Originally, the crown of the Ld_c was 'perfect except for a little wearing' (Broom & Robinson 1950: 51). The buccal view of the Ld_c is illustrated in a drawing by Broom (Broom & Robinson 1950, fig. 15C) and in a photograph (Broom & Robinson 1956, plate 3 (fig. 14)). Inasmuch as Robinson (1956) recorded the dimensions of this tooth, it would appear that it was complete until that date at least. However, at present the distolingual quadrant of the crown is

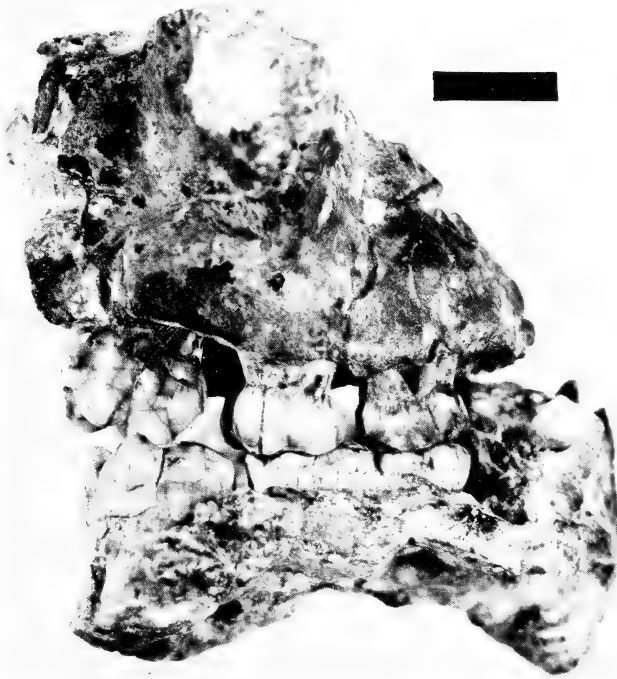


Fig. 14. Lateral view of occlusal relationship between Sts 69 and Sts 24. Note that the upper molars have been separated by postmortem diagenetic pressure, whilst the mandibular teeth are still in approximal contact. Scale in cm.

missing. It has been cracked round its entire periphery near the cervical margin with some loss of enamel (Fig. 10). The crown of the Rd_c is nearly complete except for a vertical strip of enamel over the mesial half of the buccal surface. It has a longitudinal crack through the tip.

Viewed from the buccal aspect, the crown is somewhat diamond-shaped with a high, central cuspal tip and the mesial and distal ends surmounted by smaller accessory cuspid. The mesial cuspid is situated higher than the distal cuspid. The buccal face is moderately to markedly convex mesiodistally, but it is rather flat occlusocervically except for the upper fifth of the crown, which is slightly curved. A cervical enamel prominence is not present. The buccal face mesial to the central cusp shows a faint V-shaped depression which is bounded anteriorly by a very slight enamel ridge which courses nearly vertically along the mesial edge of this surface. Occlusally, this ridge is continuous with the mesial cuspid. A larger depression is situated distal to the main cusp, and this hollow is bounded distally by a slight enamel crest which courses obliquely upwards from the cervical margin to blend into the distal cuspid. A narrow, vertical strip of hypoplastic enamel is present on the right crown.

Occlusal wear is slight in degree—it is very slightly heavier on the right crown. The tip has been reduced somewhat in height, and it shows a well-developed enamel facet with a strong lingual slope. A small patch of dentine is exposed on the lingual aspect of the tip of the Rd_c, whilst there is barely a trace of dentine exposure on the left crown. A flattened enamel facet with a strong lingual slope is present along the lingual aspect of the mesio-occlusal edge from the tip to the mesial cuspid. The cuspid has been more heavily worn (and it is slightly damaged) on the right crown. From the tip, a broad, somewhat concave enamel facet runs down the distal side of the central cusp on to the distal cuspid, where the facet is somewhat more horizontally disposed. The distal enamel facet slopes neither lingually nor buccally.

Lingually, a moderately well-developed cervical swelling is present. This swelling is skewed distally, i.e. it is considerably more prominent over the distal half of the lingual face than over the mesial (Fig. 11). A very faint cervical enamel prominence is developed over the distal moiety. The mesial marginal ridge is of moderate thickness and height, but it is short. It courses down from the mesial cuspid (where it is most strongly developed) to blend imperceptibly into the mesial part of the lingual face. The distal marginal ridge is somewhat more strongly expressed than the mesial, and it courses from the distal cuspid to the cervical swelling. A moderately deep depression is situated between the median and mesial marginal ridges. The depression between the median and distal marginal ridges is considerably deeper than the mesial groove.

The dimensions of the lower canine (side unstated) were given by Broom & Robinson (1950) as: MD, 7,0 mm; height, 7,8 mm; estimated original height, 8,5 mm. Robinson (1956) recorded the following measurements for the two crowns: left: MD, 6,4 mm; BL, 5,6 mm; height, approximately 7,6 mm; right: MD, 6,3 mm; BL, 5,6 mm; height, approximately 6,6 mm. He estimated the original height for both crowns as about 8,0 mm.

The following measurements were recorded for these two specimens by the present author:

	MD diameter (as measured)	BL diameter (as measured)	Height (as measured)	Height (est. original)
Ld _c	—	—	7,6 mm	7,8 mm
Rd _c	6,4 mm	5,7 mm	6,8 mm	7,7 mm

Mandibular first deciduous molar

The right and left first deciduous molars are represented. The right crown is complete and well preserved; the crown of the left tooth is nearly complete, with slight damage to the buccal surface.

Viewed from the occlusal aspect, the crown has a somewhat irregular, ovorectangular outline (Figs 8–9). Although the crown is worn, it is evident that at least four principal cusps are present. The protoconid appears to be the largest cusp by a considerable margin. The metaconid is well developed. The hypoconid is rather heavily worn, but it appears to have been well developed also, and probably about the same size as the metaconid. The entoconid, which

is worn also, is judged to have been somewhat reduced in size and is most certainly the smallest of the four cusps. Wear has obliterated all occlusal detail on the distal and especially distobuccal parts of the crown, and it is, therefore, not possible to ascertain with certainty whether a hypoconulid was present. The general appearance of this region of the crown indicates that a hypoconulid was probably not present, or, if present, it would have been extremely small.

Occlusal wear is moderate to heavy in degree. The left tooth is slightly more heavily worn than the right. Cuspal height has been considerably reduced, and, in general, the occlusal surface shows a distobuccally directed wear bevel. The protoconid shows a nearly flat, slightly buccally sloping wear face. A large, longitudinally elongate, ovoid dentine patch is exposed on the protoconid. The mesial end of the protoconid shows a small enamel facet (and a small dentine pit) which slopes slightly mesiobuccally. The distal end of the protoconid dentine patch is confluent with a very large hypoconid dentine exposure via a narrow isthmus; on the left crown this bridge is slightly broader. The hypoconid is covered entirely by a large, deeply concave dentine basin. This exposure is nearly triangular in shape and it continues distolingually across the crown on to the entoconid. The metaconid is the least heavily worn cusp. On the right tooth it shows a flattened enamel facet which slopes distobuccally, and on the left crown a moderate-sized dentine patch is exposed on a larger facet of similar disposition. The talonid has been reduced to a nearly flat plane, interrupted only by the dentine exposures.

Interproximal wear mesially appears to have been very slight, with only a tiny facet presented near the occlusal margin of this surface. Contact with the dm_2 distally is moderate, with a very broad, flattened plane of wear.

The mesial marginal ridge is represented by a moderately thick but low enamel crest which courses downward distolingually from the mesial end of the protoconid. The distal extremity of this ridge is considerably lower than its buccal origin, and the distolingual end is separated from the base of the mesial face of the metaconid by a narrow groove. The fovea anterior is represented by a Y-shaped groove that is both narrow and shallow. The two tines of the Y abut the lingual face of the protoconid, whilst the stem of the Y is represented by a groove between the mesial marginal ridge and the base of the protoconid. The fovea anterior is situated on the mesiolingual part of the crown, it slopes and drains lingually, and it is bounded distally by the bases of the protoconid and metaconid. It appears that these two cusps were connected by a moderately high and thick transverse ridge, the distal trigonid crest, which was incised by a shallow but broad groove. The floor of this groove, however, is considerably higher than the floor of the anterior fovea.

The lingual surface is slightly to moderately convex occlusocervically, at least over the metaconid, and a cervical enamel prominence is not present. The lingual groove is restricted to the occlusal surface where it is well developed, but the lingual face is interrupted between the metaconid and entoconid.

The buccal surface comprises two rather distinct faces—those of the pro-

toconid and hypoconid. The hypoconid surface appears to be slightly convex occlusocervically, with no development of a cervical enamel prominence. The buccal face of the protoconid is considerably larger than that of the hypoconid, and it courses downward for a considerable distance beyond the level of the hypoconid cervical line (Fig. 12). The cervical enamel margin below the protoconid continues down over the mesiobuccal aspect of the mesial root plate below the level of the radicular bifurcation, and this margin is convex downward. Also, the cervical portion of the protoconid face projects laterally beyond the level of the hypoconid surface. A moderately well-developed cervical enamel prominence is present below the protoconid. The upper part of this surface is rather flat, sloping outwards as it courses downward. The buccal groove is represented by a small, shallow depression near the occlusal margin, between the protoconid and hypoconid.

Although little of the radicular system is exposed, it is evident that it is comprised of divergent mesial and distal root plates.

Broom & Robinson (1950) recorded the dimensions of the dm_1 crown of Sts 24 as measuring: MD, 8,2 mm; BL, 7,3 mm. Robinson (1956) measured the mesiodistal and buccolingual dimensions of the right crown as 8,2 mm and 6,9 mm respectively. The left crown is, as mentioned above, slightly damaged, whilst the right tooth is complete. The dimensions of these specimens, as determined by the present author, are as follows:

	MD diameter (as measured)	MD diameter (est. original)	BL diam. trigonid (as measured)	BL diam. talonid (as measured)
L dm_1	8,3 mm	8,5 mm	(7,3) mm	(6,9) mm
R dm_1	8,2 mm	8,4 mm	7,2 mm	6,9 mm

Mandibular second deciduous molar

The well-preserved and very nearly complete crown of the right second deciduous molar is present. The only damage that this tooth has suffered is the loss of enamel (a moderately large chip) from the buccal surface of the protoconid.

Viewed from the occlusal aspect, the crown is nearly rectangular in outline; the distobuccal corner is angled somewhat by virtue of the placement of the hypoconulid. All five principal cusps are present and well developed. Occlusal wear is moderate, and it has reduced the cusps in height so that their relative sizes are somewhat obscured. It appears that the metaconid was the largest cusp, followed in decreasing order of size by the protoconid, hypoconid, entoconid, and hypoconulid.

Occlusal wear has reduced the buccal cusps to a nearly flat, horizontal plane, whilst the metaconid and entoconid retain fairly high, sharp tips. Wear is heaviest on the mesiobuccal quadrant of the crown, where the protoconid has been reduced to a large, ovoid and rather deeply concave dentine exposure. The mesial end of the occlusal surface has been worn flat and a very narrow, transverse dentine strip here is continuous with the protoconid dentine exposure. The hypoconid displays a somewhat smaller, ovoid and concave patch of

dentine. The hypoconulid has been reduced to a low, rounded hump with a small dentine pit on its tip. The entoconid shows a large, concave enamel facet. The metaconid, which is the least heavily worn of all, shows two enamel facets. Neither lingual cusp shows any dentine exposure.

Interproximal contact mesially with the dm_1 is, as mentioned above, moderate. A small, flattened distal facet indicates slight interproximal contact with the first permanent molar.

Although occlusal wear has obliterated much of the morphological detail, it is evident that a broad metaconid-hypoconid contact is present. The metaconid extends distally beyond the level of the protoconid, thus, the mesiobuccal groove is situated mesial of the level of the lingual groove. The primary fissure pattern is arranged in a rather symmetrical Y-shaped configuration. The distal marginal ridge appears to have been relatively narrow. It is low and deeply incised in its middle. The fovea posterior is represented by a small pit which is bounded mesially by the postentocristid, which is higher (even though worn) than the distal marginal ridge.

The lingual surface is very slightly convex occlusocervically, and a cervical enamel prominence is not present. The lingual groove is very short and narrow.

The buccal surface is, at least over the remaining cervical portion of its height, slightly more convex occlusocervically than the lingual face. The mesiobuccal groove is represented by a shallow, narrow and vertical fissure which ends rather abruptly a few millimetres above the cervical margin. The distobuccal groove is considerably less well developed than the mesiobuccal, and it is represented by a short, shallow depression. Numerous, very tiny hypoplastic pits cover much of the buccal surface of the hypoconid.

The principal measurements of this crown were determined by Broom & Robinson (1950) as: MD, 10,8 mm; BL talonid, 9,0 mm. Robinson (1956) measured the same dimensions of the specimen as: MD, 10,7 mm; BL talonid, 9,0 mm. The present author has recorded the following measurements for this tooth:

	MD diameter (as measured)	MD diameter (est. original)	BL diam. trigonid (as measured)	BL diam. talonid (as measured)
Rdm ₂	10,8 mm	10,9 mm	8,8 mm	9,0 mm

Permanent dentition (Figs 8-9, 12-13)

Mandibular central permanent incisor

The complete, well-preserved crown and a short segment of the root of the unerupted right I_1 are present. A bit of enamel has been damaged on the distocervical aspect of the buccal face and along the distal cervical margin.

The mesial and distal corners of the incisal edge are rather sharply angulated, and both of these extremities are surmounted by moderately large, sharp mammelons. The incisal edge is horizontal. It supports some five mammelons, of which the two end and the median, or central, are moderately large, whilst the other two are slightly smaller.

Viewed from the labial aspect, the crown has a tapered outline with the mesiodistal width considerably greater at the incisal edge than the cervical margin. The labial surface is slightly convex incisocervically, and it appears that no cervical enamel prominence is present. The upper two-thirds of the labial face is covered by numerous faint perikymatous lines.

Lingually, there is a moderately well-developed, centrally or symmetrically situated basal swelling. This swelling does not support a tubercular structure. The mesial and distal margin ridges are faintly developed over the incisal third of this face, and a median ridge is not present. The lingual face is moderately concave incisocervically but flattened mesiodistally.

Broom & Robinson (1950) recorded the following measurements of the crown: MD, 6,2 mm; BL, 6,3 mm; height, 11,8 mm. Robinson (1956) obtained the following measurements: MD, 6,3 mm; BL, 6,1 mm; height, 11,7 mm. The present author has determined the measurements of this crown as:

	MD diameter (as measured)	BL diameter (as measured)	Height (as measured)
RI ₁	6,2 mm	6,1 mm	11,6 mm

Mandibular lateral permanent incisor

The nearly complete crowns of both the left and right teeth are preserved. A short segment of developing root is attached to both crowns.

The right tooth is cracked along a plane which transects the lingual cervical margin and cuts through the cervical third of the buccal face, and a relatively large chip of enamel has broken away from the labial surface at the level of this crack. The left crown is complete and undamaged.

The mesial corner of the incisal edge is considerably higher than the distal. The mesial end is very slightly rounded and it is surmounted by a rather large mammelon. A relatively deep cleft at the distal end of this mammelon separates it from a very large, mesiodistally elongate central mammelon which dominates the incisal edge. The central mammelon is highest mesially and it slopes downward to its distal end where a sharp groove separates it from a moderately sized mammelon at the distal extremity of the incisal edge.

The labial surface is very slightly convex incisocervically. A cervical enamel prominence is not present. Viewed from this aspect, the crown is tapered in outline, with the mesiodistal diameter greater incisally than cervically. On the left crown, a slightly elevated, moderately thick crest of enamel runs up the distal edge of the labial face from approximately 4,0 mm above the cervical line to just below the distal mammelon. Both the upper and lower extremities of this ridge blend gradually into the labial face. On the right crown the same ridge is only very faintly demarcated.

Lingually, a rather prominent basal swelling is present, and there is no cervical enamel prominence. The basal swelling is centrally or symmetrically situated and it does not support a tubercular structure. The mesial marginal ridge is only slightly developed, and it runs downward from the mesial mammelon and terminates just above the basal swelling. The distal marginal ridge is

somewhat more elevated and thicker than the mesial, and it courses from the distal mammelon and terminates just above the basal swelling. The lingual surface is moderately concave incisocervically, but relatively flat mesiodistally.

Broom & Robinson (1950) recorded the following measurements for this tooth (side not stated): MD, 7,3 mm; height, 13,0 mm. Robinson (1956) reported the dimensions of this tooth (side not stated) as: MD, 7,3 mm; BL, 6,8 mm; height, 13,0 mm. The principal dimensions of these crowns, as recorded by the present author, are as follows:

	MD diameter (as measured)	BL diameter (as measured)	Height (as measured)
LI ₂	7,4 mm	7,0 mm	12,6 mm
RI ₂	7,3 mm	7,0 mm	12,5 mm

Mandibular anterior premolar

The nearly complete, well-preserved crowns of both the left and right P₃'s are present. In both cases the cervical margins lingually (LP₃) and mesiolingually (RP₃) have suffered post-mortem damage. This damage is somewhat more severe on the right crown. The buccal cervical margins of the crowns appear to be incompletely formed—it is judged that only a short segment of enamel would have been deposited here—but otherwise the crowns are evidently completely formed. In fact, a short segment of root is present along the distal aspect of the left tooth. The two crowns are nearly identical in morphological detail. Broom & Robinson (1950: 44) provided a very brief description of this tooth, but Robinson (1956) considered it to be incompletely developed and therefore did not include it in his sample of Sterkfontein premolars.

Viewed from the occlusal aspect, the crown is somewhat trapezoid in outline. The buccal side of the crown is considerably longer mesiodistally than the lingual side, and whilst the distal edge follows a nearly straight transverse course, the mesial border slopes distally from buccal to lingual. The crown is dominated by a very large buccal cusp and a considerably smaller lingual cusp.

The buccal cusp extends from the front of the crown nearly to the distal end, where it is separated by a deep cleft from a moderately well-developed distostylid at the buccal extremity of the distal marginal ridge. The tip of the main buccal cusp is situated approximately midway between the mesial and distal sides of the crown, and relatively sharp crests course mesially and distally from its summit. A well-developed bifurcating crest runs distolingually from the tip of the buccal cusp.

The lingual cusp is somewhat lower and much smaller in area than the buccal cusp. It is situated on the mesiolingual quadrant of the crown and its tip is displaced mesial to the mid-crown transverse axis which bisects the buccal cusp. A moderately thick cingulum surrounds the distolingual aspect of the base of the lingual cusp. This cingulum arises from the lingual aspect of the lingual cusp's tip and slopes downward to form a low, broad shelf. A slight median ridge, which drops swiftly, and a sharp distal crest course from the tip of the lingual cusp.

A small accessory cuspid is present at the mesial end of the buccal cusp. This cuspid is incompletely separated from the main buccal cusp and it represents the buccal extremity of the mesial marginal ridge. The mesial marginal ridge comprises a buccal part from the mesial accessory cuspid and a lingual part from the lingual cusp; these crests course downward and converge at the middle of the mesial aspect of the crown, where the mesial marginal ridge is the same height as the floor of the fovea anterior.

The fovea anterior is represented by a moderately large basin which is completely enclosed distally by a transverse ridge formed by the crests from the buccal and lingual cusps. This ridge is shallowly incised in its middle by a narrow groove.

The distal marginal ridge, which is moderately thick, descends from the tip of the distostylid to the distal side of the base of the lingual cusp. At its lingual extremity the ridge supports a small cuspid. The ridge continues round the distolingual side of the lingual cusp as a cingulum. The fovea posterior, which is completely enclosed by the distal marginal ridge and the median transverse ridge, is represented by a relatively large, deep basin.

The lingual surfaces on both crowns are damaged. The buccal surface, in so far as it is developed, is rather flat, sloping outwards occlusocervically. The mesial portion of this face shows a shallow depression bounded mesially by a slight, vertical enamel crest which ends occlusally in the mesial accessory cuspid. Distally, a moderately expressed vertical ridge rises to the distal cuspid. This ridge is separated by a relatively deep groove from the remainder of the buccal surface.

Broom & Robinson (1950) recorded the mesiodistal diameter of the crown as 9,4 mm and the incompletely developed buccolingual diameter as 10,1 mm. Further development would have added enamel to the buccal and lingual cervical margins, but the mesiodistal dimension would probably have been unaffected. The dimensions of these two crowns, as determined by the present author, are as follows:

	MD diameter (as measured)	BL diameter (as measured)	BL diameter (est. complete)
LP ₃	9,4 mm	10,1 mm	?
RP ₃	9,3 mm	10,0 mm	?

Mandibular posterior premolar

The immature and incomplete crown of the right P₄ is present. As preserved, the crown consists only of part of the buccal and lingual cusps and the fovea anterior. It is evident that the buccal cusp is larger than the lingual, which is situated mesiad of the mid-crown transverse axis which bisects the buccal cusp. An incipient mesiobuccal accessory cuspid is present at the mesial extremity of the buccal cusp. The mesial marginal ridge is very low; it forms a shelf-like extension of the floor of the fovea anterior.

It is not possible to record any useful measurements for this specimen.

Mandibular first permanent molar

The complete, well-preserved crown and part of the radicular system of the right M_1 are present.

Viewed from the occlusal aspect, the crown is nearly rectangular in outline. All five principal cusps are present and well developed. The metaconid is judged to be the largest cusp, followed very closely in size by the protoconid. The hypoconid and entoconid, which are nearly equal in size, are slightly smaller than the trigonid cusps, and the hypoconulid is the smallest cusp.

It is evident that this tooth had just reached occlusal contact with the M^1 at the time of death. Occlusal wear is restricted to a slight, flattened facet on the tip and mesial aspect of the protoconid.

The mesial marginal ridge is extremely low and for most of its length it is no higher than the floor of the fovea anterior. Several very small cusplids are present in the middle of the mesial aspect of the fovea. The fovea is represented by a relatively large, flat depression bounded distally by a rather thin, low transverse crest between the metaconid and protoconid. This crest is deeply incised by a very narrow groove.

A moderately broad metaconid-hypoconid contact is present. The lingual groove is situated slightly distal of the level of the mesiobuccal groove, and thus the Y pattern formed by the main occlusal fissures is not symmetrically disposed.

The distal marginal ridge is very poorly developed. It is represented by a slight crest from the tip of the hypoconulid which courses cervically over the distal surface of the crown. The fovea posterior is represented by a small pit which continues over on to the distal surface of the crown as a short, narrow vertical groove. The postentocristid is low but moderately thick; it is incised by a deep and narrow groove.

The main crests of the metaconid, entoconid and hypoconid bifurcate or trifurcate, imparting a slightly crenulate appearance to the occlusal surface.

The lingual surface is rather flat and is nearly vertical occlusocervically. The lingual groove is narrow, and extends vertically over about half the height of the crown. A cervical enamel prominence is not present.

The buccal surface is slightly convex occlusocervically, especially over the upper half of its height. A very slight cervical enamel prominence is apparent. The mesiobuccal groove is deep and courses vertically over about two-thirds of the crown height. It ends abruptly. The distobuccal groove is deep; it is rather broad but shorter than the mesiobuccal groove. The distobuccal groove also ends abruptly. A flattened area is present on the buccal aspect of the protoconid, and this region is bounded below by a flat enamel shelf. No evidence of perikymatous or hypoplastic enamel is shown by either the buccal or the lingual surfaces.

Broom & Robinson (1950) recorded the dimensions of this crown as: MD, 13,3 mm; BL, 11,3 mm. Robinson (1956) measured it as being: MD, 13,1 mm; BL, 11,2 mm. The principal measurements of this tooth, as measured by the present author, are as follows:

	MD diameter (as measured)	BL diam. trigonid (as measured)	BL diam. talonid (as measured)
RM ₁	13,3 mm	11,3 mm	11,2 mm

SPECIMENS STS 24/69/70 COMPOSITE

The reasons for associating the Sts 69 and 70 maxilla have been discussed. Equally strong evidence exists for associating these two specimens with the mandible and dentition represented by Sts 24. Firstly, the state of preservation, the colour, and the staining of the enamel of the teeth contained in the maxillary and mandibular specimens are very similar. Secondly, the developmental status and eruption of the permanent teeth in these specimens are compatible with their having derived from a single individual. Thirdly, the general occlusion of the deciduous and first permanent molars of the Sts 69 and Sts 24 specimens is very good (Fig. 14). The two upper and two lower deciduous molars do not afford a simultaneous precise fit because the maxillary molars have been spread apart through diagenetic deformation, whilst the lower molars still remain in approximal contact. However, the occlusal relationships between the individual molars are excellent. Finally, the degree, pattern and details of occlusal wear between the corresponding upper and lower molars are too close for this to be a chance association.

Besides adding several well-preserved and complete deciduous and permanent teeth to the collection from Sterkfontein, this specimen provides the most complete maxilla of an australopithecine child from South Africa, save for the Taung skull. Finally, this composite specimen represents the only associated and occluding maxillary and mandibular cheek teeth of a 'gracile' australopithecine child from Sterkfontein. In fact, this specimen provides the most complete associated gnathic and dental remains of a juvenile australopithecine from South Africa, apart from the Taung skull.

The mandibular specimen and its associated teeth retain its original catalogue number, Sts 24, whilst the numbers of the two maxillary fragments (Sts 69 and Sts 70) and their associated teeth have been changed—together they are now referred to as Sts 24a.

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I am grateful to Drs C. K. Brain and E. S. Vrba for permission to further prepare and describe specimens in their care. This paper benefited from the comments and advice of Drs T. D. White and B. A. Wood. Mr A. R. Hughes and Mr H. Thackwray assisted with photography. This work was supported by a grant from the Senate Research Committee, University of the Witwatersrand.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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AUSTRALOPITHECUS AFRICANUS
(MAMMALIA, PRIMATES) FROM MEMBER 4,
STERKFONTAIN FORMATION, TRANSVAAL

PART 5

JULY 1981

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ANNALS

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(continued inside back cover)

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THE POSTCRANIAL SKELETON OF
ROBERTIA BROOMIANA, AN EARLY
DICYNODONT (REPTILIA, THERAPSIDA)
FROM THE SOUTH AFRICAN KAROO

By

G. M. KING

Cape Town Kaapstad

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THE POSTCRANIAL SKELETON OF *ROBERTIA BROOMIANA*, AN EARLY DICYNODONT (REPTILIA, THERAPSIDA) FROM THE SOUTH AFRICAN KAROO

By

G. M. KING

Department of Zoology and University Museum, Oxford

(With 15 figures)

[MS. accepted 6 January 1981]

ABSTRACT

The postcranial skeleton is described. Some comparison with later dicynodonts is made.

Where possible the muscles of the pectoral and pelvic girdles are reconstructed. The forelimb took up a sprawling position relative to the body. The biceps, brachialis, coracobrachialis and pectoralis muscles were all well developed as adductors. Limb extension by the powerful triceps was probably an important contribution to the otherwise short stride. The supracoracoideus probably inserted on the medial side of the scapula, passing beneath the everted acromion process. It is argued that development of the acromion process might have been in relation to the use of the clavicle as a movable rod, rather than an inflexible brace, in the girdle.

The femur took up a sprawling position in the body. The main retractor muscle was the iliofemoralis. The position of the head of the femur on the anteromedial extremity of the bone is seen as an adaptation for lengthening the stride of the hind limb. The ilium is not produced far anteriorly as in later dicynodonts, and the trochanter major is not well developed. It is postulated that in later dicynodonts the further development of the trochanter major and the iliofemoralis was to produce long axis rotation in the stride.

In the vertebral column flexibility in a lateral plane was provided for by the flattened zygapophyses.

It is suggested that *Robertia* was a lizard-like animal, possibly partly insectivorous.

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INTRODUCTION

The dicynodonts, a group of herbivorous mammal-like reptiles, probably arose at some time in the Lower Permian. After a period of considerable success in terms of both species number and diversity, most forms became extinct at the

end of the Permian. Only one major lineage survived into the Triassic, undergoing a small adaptive radiation.

The earliest member of the Dicynodontia (*sensu* Romer 1966) is *Eodicynodon oosthuizeni* (Barry 1974), reputedly from Ecca beds of South Africa. These beds lie at the base of the fossil-bearing Beaufort Series of the South African Karoo sediments, and are generally considered to be non-fossiliferous. Before the discovery of *Eodicynodon* the earliest dicynodonts were known from the lowermost zone of the Beaufort Series, the *Tapinocephalus* Zone. There is some dispute over the exact age of *Eodicynodon* (A. W. Keyser 1978 pers. comm.), but it seems that even if it is actually a *Tapinocephalus* Zone form, it is from a lower level in that zone than any other fossil.

Eodicynodon retains several primitive features relative to other dicynodonts: the secondary palate is short, the premaxillae are paired, the vomers are paired, there is a lateral pterygoid flange. No postcranial remains have been recovered.

Several genera of dicynodonts have been described from the higher levels of the *Tapinocephalus* Zone in South Africa. Even at this early stage the dicynodonts had diversified, although remaining small and being characterized by the possession of postcanine teeth. It is likely that of the nine or so genera described in the literature as *Tapinocephalus* Zone forms, probably about five are actually valid. Work in progress by Cluver & King attempts to establish these groups. One of the groups is founded on *Robertia broomiana* (Boonstra 1948; Toerien 1953) and contains *Tapinocephalus* Zone forms having a few small postcanine teeth, a notched palatal rim with a maxillary blade posterior to the notch and a lateral dentary shelf which tends to occlude the intra-mandibular fossa. This group contains the only specimens of *Tapinocephalus* Zone postcranial material which can be assigned to a genus and species, being found in association with cranial material.

The material in question (SAM-11885) is that referred to by Boonstra (1966) as 'Endothiodontid. A number of fairly complete skeletons. Michau's Request, Beaufort West. Low *Tapinocephalus* Zone.' Femur, lower forelimb and lower hind limb are figured. The skulls included in SAM-11885 have the following features in common with the type of *Robertia broomiana*: postcanine teeth (Fig. 1:t), the maxillary notch (Fig. 1:n), the lateral dentary shelf (Fig. 1:d s), and reduced palatines (Fig. 1:pal). (In all figures a broken line indicates the reconstruction of a damaged area, unless otherwise specified.) They are here assigned to that genus and species.

A complete description and detailed discussion of the postcranial skeleton of *Robertia* is warranted since it represents the earliest dicynodont postcranial material known. Previous descriptions of postcranial skeleton (excluding Boonstra 1966) have been concerned with later fossils, for example *Kingoria* (Cox 1959), *Cistecephalus* (Cluver 1978), *Kawingasaurus* (Cox 1972), *Dicynodon trigonocephalus* (King 1981), *Tetragonias* (Cruickshank 1967), *Kannemeyeria* (Pearson 1924) and *Placerias* (Camp & Welles 1956). Various aspects of the

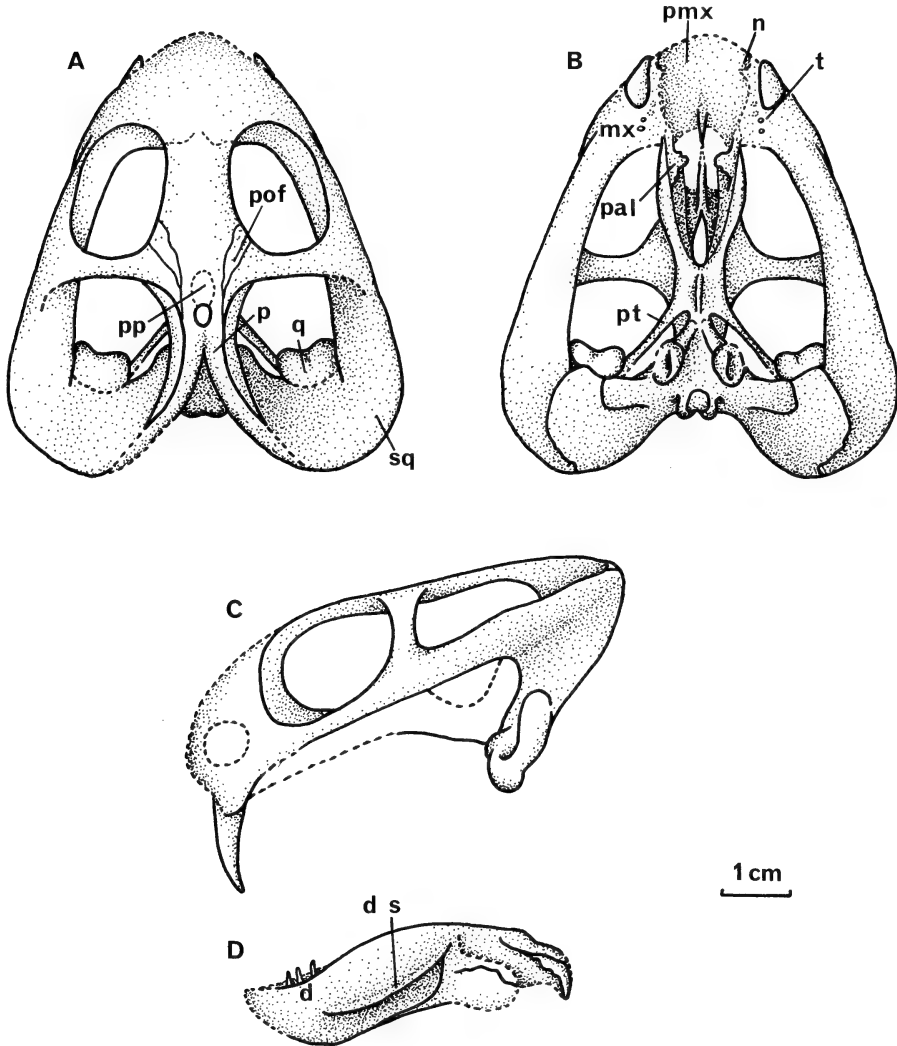


Fig. 1. *Robertia broomiana*, skull and lower jaw. A. Skull dorsal. B. Skull palatal. C. Skull lateral. D. Lower jaw lateral. (Reconstructed from casts 1 and 2.)
(For abbreviations see p. 229.)

skeleton of such dicynodonts are extremely specialized when compared to other therapsids (see also Parrington 1955) and it is hoped that study of an early form may shed light on the processes and pathways which brought about these specializations. Information on their postcranial anatomy may also help in the interpretation of the kinds of habitats which these early forms occupied and indicate why the dicynodonts did not apparently radiate explosively until later on in the *Cistecephalus* Zone.

MATERIAL

The material consists of twelve latex casts in the South African Museum, Cape Town (SAM-11885). The original bones had been dissolved out of the intractable matrix by using a strong acid, so that the resulting casts are positive impressions. The preservation of the bones was in parts excellent, and the casts represent the bone detail very well. At least three partial skeletons were present in several blocks of matrix. There is very little variation between the skeletons, making it entirely reasonable that they represent one species. There are several runs of articulated vertebrae, and several associated girdles with limb bones. The distribution of skeletal elements in the various casts is as follows:

- Cast 1. Partial skull and lower jaw. Radius, ulna and manus.
- Cast 2. Skull and lower jaw in palatal view. Neck vertebrae.
- Cast 3. Lower jaw. Scapula, humerus, radius and ulna, carpals. Dorsal aspect of a sequence of vertebrae. Ribs.
- Cast 4. Humerus, interclavicle, partial clavicles.
- Cast 5. Two scapulae, partial coracoid and precoracoid. Humerus. Disarticulated vertebrae and ribs.
- Cast 6. Sequence of mid-dorsal ribs and vertebrae.
- Cast 7. Femur (1), fibula, incomplete pes. Tail vertebrae, right and left ilium and pubo-ischiadic plate, two incomplete sacral vertebrae. Femur (2).
- Cast 8. Proximal end of femur and dorsal edge of ilium which are counterparts of femur (2) and left ilium of cast 7. Run of vertebrae and ribs.
- Cast 9. Femur, pes, fibula and tail vertebrae which are counterparts of femur (1), fibula, pes and tail vertebrae of cast 7.
- Cast 10. Clavicle, a sequence of vertebrae and some ribs. Distal end of a humerus; radius and ulna, carpals.
- Cast 11. Humerus, radius and ulna, carpals which are counterparts of cast 10.
- Cast 12. Disarticulated ribs. Partial scapula and coracoid. Sternum. Humerus (3) and radius and ulna. Humerus (4) in dorsal view.

Two other dicynodonts have been used for comparative purposes. One is a medium-sized *Daptocephalus* Zone (*sensu* Kitching 1977) dicynodont, *Dicynodon trigonocephalus* (King 1981) which has a virtually complete postcranial skeleton. The other (TSK 83, a specimen from T. S. Kemp's collection housed in the Oxford University Museum) is a collection of several partly-disarticulated small skeletons from the *Daptocephalus* zone of Zambia (Madumabisa Mudstones horizon). These conform to Cluver & Hotton's (1981) definition of *Dicynodon*, having a dorsal dentary sulcus, no lateral dentary shelf, an unnotched maxillary rim, and dentary tables. The specimens may be immature individuals, being small, having unerupted tusks, and open sutures.

In the following description and analysis the positions of the origins and insertions of muscles have been reconstructed with reference to Romer (1922). The possibilities of movement of the limbs were investigated by manipulating plasticine models of the bones.

DESCRIPTION AND FUNCTIONAL ANATOMY

FORELIMB AND PECTORAL GIRDLE

Four well-preserved scapulae are present (Fig. 2). The dorsal blade is rather narrow. It curves medially and its lateral surface is concave anteroposteriorly. The anterior edge is thick and drawn up into a prominent ridge facing laterally (Fig. 2: r). The ridge continues ventrally into the acromion process (Fig. 2: ac p) which is large and strongly everted. The medial side of the acromion process and the body of the scapula adjoining it are hollowed out into a shallow fossa (Fig. 2: s fo). The anterior edge of the scapula just below the acromion process is smooth and this, together with the eversion of the process, would allow the supracoracoideus muscle to pass on to the medial side of the scapula and attach into the shallow fossa there. The medial surface of the scapula is strongly convex anteroposteriorly and drawn up into a ridge at the height of the convexity (Fig. 2: m r). This may mark the division between the origins of the supracoracoideus and subscapularis muscles. Since the ventral part of the scapula blade is so slender, neither of these muscles could have had an extensive origin here.

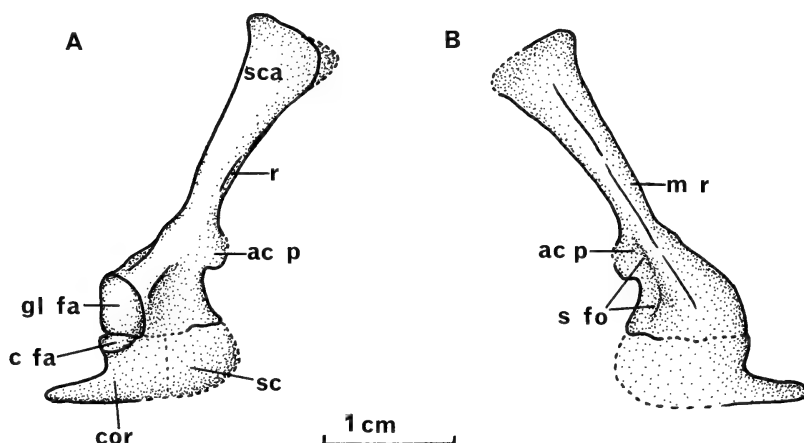


Fig. 2. *Robertia broomiana*, shoulder girdle. A. Lateral. B. Medial. (Reconstructed from casts 5 and 12.)

Below the acromion process the scapula fans out to form the articulation with the coracoid, and the glenoid. The scapula glenoid facet (Fig. 2: gl fa) is approximately circular. It faces downward, backward and slightly outward if the blade of the scapula is tilted slightly forward (Fig. 2). The facet is shallowly concave dorsoventrally and convex anteroposteriorly. The coracoid is well preserved only in medial view but the glenoid facet (Fig. 2: c fa) appears to face backward and upward. The precoracoid appears to be of the usual dicynodont conformation but it is badly preserved and the precoracoid foramen is not evident.

Much of the interclavicle (Fig. 3b) is preserved. It is a rectangular sheet of bone drawn up into a low boss in the midline of the ventral surface (Fig. 3B: b). On either side of the boss the surface may be hollowed out into a very shallow and indistinct fossa, presumably for the attachment of the pectoralis muscles. In one specimen the proximal ends of the clavicles are preserved *in situ* on the interclavicle (see Fig. 3B). The proximal end of the clavicle is flattened and spoon-shaped, bearing a distinct ridge (Fig. 3B: r) which continues on to the

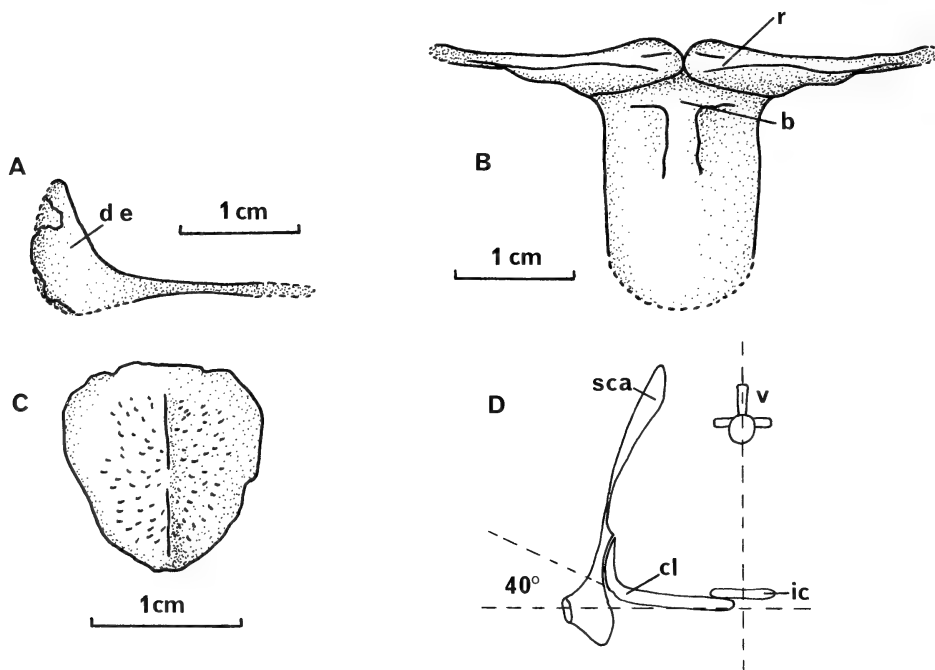


Fig. 3. *Robertia broomiana*, clavicle, interclavicle and sternum. A. Clavicle anterior. B. Clavicles and interclavicle ventral. C. Sternum ventral. D. Diagram to show the relative orientations of the elements of the girdle (explained further in the text), anterior. (Reconstructed from casts 4, 10, and 12).

shaft of the bone. The distal end is also expanded, in a direction at right angles to the expansion of the proximal end. The distal end is approximately triangular (Fig. 3A: d e), very extensive and rather robust.

Much of the sternum is present, though poorly preserved (Fig. 3C). It would seem to take the form of an oval plate which tapers slightly towards its posterior end. It bears a slight median ridge. The bone surface is uneven in texture, bearing irregular striations. The posterior and anterior edges are somewhat thickened. Other edges are not sufficiently well preserved to determine thickness, or whether rib articulations were present.

The humerus (Fig. 4) is well preserved. The distal and proximal ends of the bone are expanded in typical dicynodont fashion. The head (Fig. 4: hd) faces

medially and somewhat dorsally but is not pronounced. Anterior to the head the bone is drawn into the deltopectoral crest (Fig. 4: d p c). Presumably the deltoideus muscle inserted mainly on the dorsal surface of the crest, while the pectoralis muscles inserted on the rugose ventral surface (Fig. 4: v s). On the dorsal surface the crest is marked off abruptly from the shaft of the bone by a pronounced ridge (Fig. 4C: r) posterior to which is a triangular fossa (Fig. 4C: t fo). The dorsal surface is, therefore, quite unlike that of *Dicynodon trigonocephalus* (Fig. 4D) where there is no such fossa in the middle of the bone. Instead, in *D. trigonocephalus* there are a shallow fossa on the posterior margin of the bone and a strong tubercle (Fig. 4D: tub) which have been interpreted as

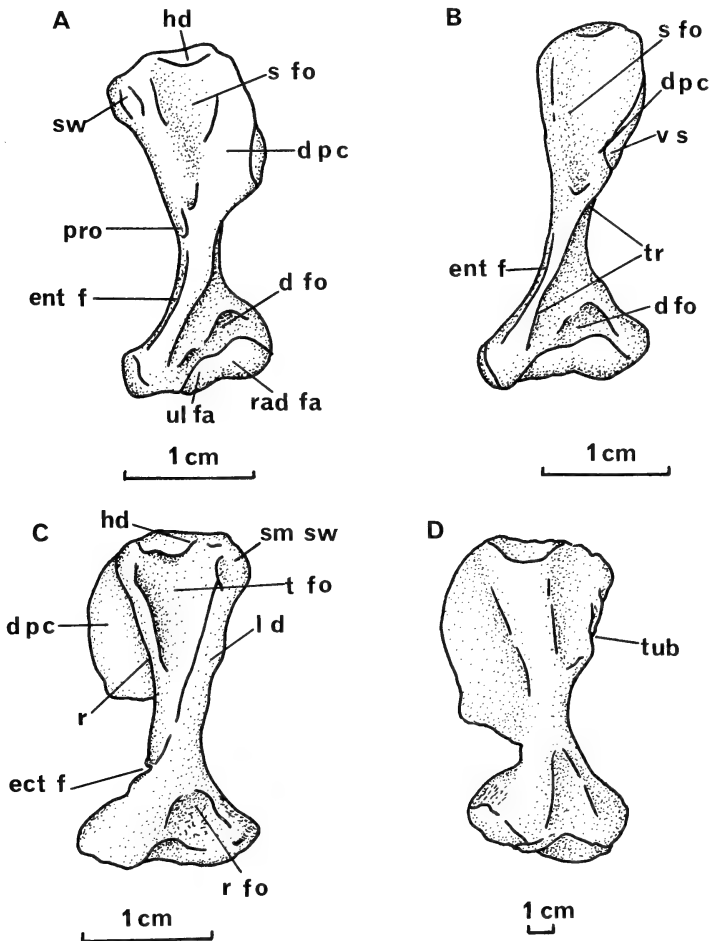


Fig. 4. *Robertia broomiana*, left humerus. A. Proximal ventral. B. Distal ventral. C. Proximal dorsal. D. Humerus of *Dicynodon trigonocephalus* in proximal dorsal view. (A reconstructed from cast 4; B reconstructed from cast 5; C reconstructed from cast 12, humerus 4.)

the attachment site of the triceps (King 1981). No tubercle is present on the humerus of *Robertia* and the attachment of the triceps humeralis lateralis is here taken to be in the extensive triangular fossa. Two small swellings are found on the posterior edge of the bone, one near the head of the bone which encroaches on the dorsal surface (Fig. 4C: sm sw), and the other more distal (Fig. 4C: l d). These may represent the insertions of the subscapularis and latissimus dorsi, respectively.

The ventral surface of the proximal end is excavated into a shallow but extensive fossa (Fig. 4A–B: s fo) between the deltopectoral crest and the posterior margin. This probably represents the insertion of the coracobrachialis muscle. Posterior and distal to this fossa is a marked protuberance (Fig. 4A: pro) possibly indicating the coracobrachialis longus insertion. The posteromedial corner of the posterior margin of the ventral surface is also rather swollen and striated (Fig 4A: sw). This may mark the encroachment on the ventral surface of the insertion of the subscapularis muscle.

The distal ventral surface bears an entepicondylar foramen (Fig. 4A–B: ent f). In addition, several humeri also show evidence of the ectepicondylar foramen (Fig. 4C: ect f). In dorsal view a notch leading from the anterodorsal surface to the ventral surface can be seen. The notch is continued either side by a groove running from the dorsal surface in a ventral, anterior, and distal direction.

The facets for articulation of the radius and ulna (Fig. 4A: rad fa, ul fa) are largely ventral. Anterior to these facets is a deep and well-defined fossa (Fig. 4A–B: d fo). This may indicate the site of insertion of ligamentous connections to the lower limb.

The position of the brachialis inferior is shown quite clearly on several specimens, being delimited by the pronounced dorsal ridge which separates the triceps lateralis fossa from the deltopectoral crest. The brachialis origin presumably starts on the ventral distal surface anterior to the entepicondylar foramen. It passes proximally and dorsally on to the body of the deltopectoral crest to lie posterior to the deltoideus insertion. The whole of the area of origin described forms a smooth and continuous trough (Fig. 4B: tr).

On the dorsal surface a fossa (Fig. 4C: r fo) is present near the posterior margin of the bone. The surface of the fossa is rough and the posterior and distal edges of the bone are deeply striated. This would be a reasonable position for the origin of the triceps humeralis medialis.

The radius and the ulna are shown in Figure 5. In the following description it is assumed that the bones are oriented at right angles to the humerus. Each is a slender element approximately three-quarters the length of the humerus. The ulna bears a weak olecranon process (Fig. 5B–C: o p). The anterior surface of this bone is excavated into an extensive fossa proximally (Fig. 5B: pr fo). The medial edge of this is continued ventrally as a pronounced ridge (Fig. 5B: r) forming the medial edge of the bone over most of its length, but turning on to the anterior surface far ventrally. The proximal fossa extending down from the olecranon process was presumably for the triceps insertion, while the long ridge

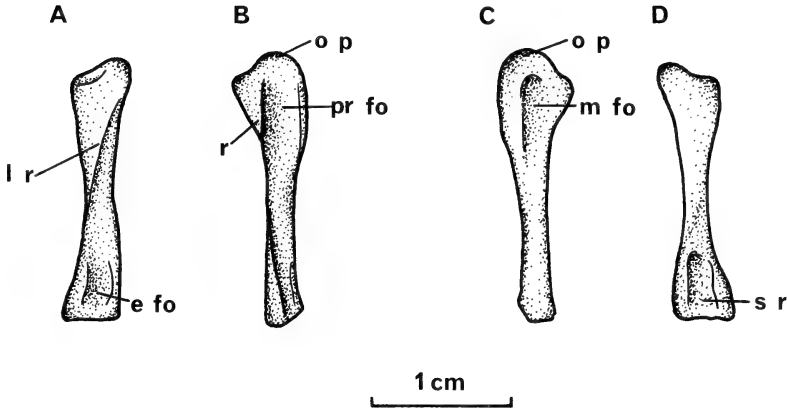


Fig. 5. *Robertia broomiana*, right radius and ulna. A. Radius anterior. B. Ulna anterior. C. Ulna posterior. D. Radius posterior. (Reconstructed from cast 3.)

probably took the biceps insertion. The posterior surface of the ulna also bears a marked excavation proximally (Fig. 5C: m fo), possibly the insertion of an ulnar flexor from the entepicondyle.

The distal end of the ulna is approximately oval, concave anteroposteriorly and convex mediolaterally. The distal end of the radius is greater in area and flatter.

The radius itself bears a distinct elongate fossa (Fig. 5A: e fo) on its anterior distal surface. A low ridge runs along the anterior surface from the proximal lateral to the distal medial corner (Fig. 5A: l r). This probably was the site of insertion of the brachialis inferior. A much shorter ridge runs along the posterior surface of the distal end (Fig. 5D: s r).

The forefoot is well represented but not complete. Figure 6 shows a reconstruction based on all the specimens preserved. Of the carpus an ulnare, a radiale and an intermedium can be identified. A small bone near to the radius of one specimen may represent a pisiform. The best-preserved carpus shows three more distinct bones, two of which are probably centralia, but it is difficult to be certain. One of the elements (Fig. 6: ce?) is rather large and may indicate fusion of two centralia.

Metacarpals I to V are present. They are elongate bones, very slightly flattened dorsoventrally. Number I is significantly smaller than the others. No complete digit V is present but all others are, and the phalangeal formula is 2-3-3-3-(?3). No reduced or fused phalanges are apparent. Each terminal phalanx is a blunt claw, displaying a pronounced boss on its plantar surface (Fig. 6B: b). The phalanges in each digit increase in size proximally. The phalanges of digit III are the longest, indicating that the hand might have been approaching a symmetrical condition.

The hand gives the impression of being long-fingered and flexible. In one specimen the metacarpal and phalanges of the longest finger together are as long

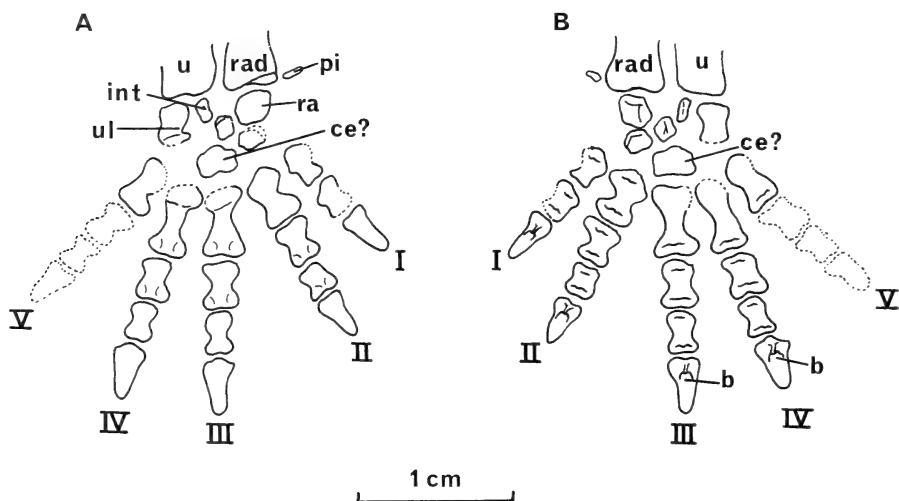


Fig. 6. *Robertia broomiana*, right forefoot. A. Dorsal. B. Plantar. (Reconstructed from casts 1, 3, and 11.)

as the radius. Such a large hand might have acted simply as a platform to support and stabilize the body, but, although long, the hand is not particularly broad. The stout claws may rather suggest a tearing or scratching function.

Discussion

The above morphological and anatomical considerations, when subjected to a functional analysis, indicate that the forelimb took up a primitive sprawling position relative to the body, and that, on the whole, the muscle pattern of the forelimb and girdle was conservative. However, many of the specialized features of later dicynodonts are already present in the *Tapinocephalus* Zone form.

The orientation of the glenoid depends on how the scapula is oriented in the body. This is difficult to deduce in a disarticulated skeleton, but one clue is the position and direction of the clavicle and interclavicle. The shaft of the clavicle leaves the interclavicle in the midline, either horizontally or at a very small angle (Fig. 3D). The distal part of the clavicle then turns backward (about 40°) while expanding dorsally. The posterodistal edge of the bone is a smooth arc congruent with the arc of the scapula anterior edge above the acromion process. Because of the orientation just described, the clavicle arc is positioned sloping slightly forward in the body and therefore the scapula edge must do the same. The overall orientation of the scapula is, therefore, with the blade sloping forward at an angle of approximately 60° to the horizontal, and curving dorsomedially. The glenoid facet will then face mostly laterally and also posteriorly. When the humerus is articulated in the glenoid it takes up a sprawling position. An erect or semi-erect position is not possible because the head of the bone is mainly dorsal and in the middle of the proximal end. In the sprawling

position a rather limited protraction–retraction arc is possible before the head is disarticulated or before the deltopectoral crest touches the girdle. For the latter reason, also little long axis rotation is possible. Elevation and adduction of the distal end of the bone does seem to be possible.

The facets on the humerus for articulation with the radius and ulna are almost completely ventral, indicating that the antebrachium was positioned at right angles to the humerus as would be expected in a sprawling-gaited animal.

With the forelimb so positioned, there is a tendency for the animal's body to collapse through the girdle under the action of gravity unless strong postural muscles are present. Such muscles can prevent collapse only if the angle between the two elements that are collapsing is increasing, as then shortening of a muscle can restore the former relationship of the two elements. Therefore, in a sprawling-gaited animal the postural muscles important in preventing collapse are the ventral adducting muscles, the biceps, brachialis, coracobrachialis and pectoralis. The sites of attachment in *Robertia* show that these muscles were all very well developed (Fig. 7A, C–E). The triceps does not have this kind of postural function, neither do the dorsal muscles such as the deltoideus, supracoracoideus or subscapularis. The supracoracoideus would have protracted the limb, the deltoideus elevating it. The latissimus dorsi presumably played a part in retracting the limb, helped by the subscapularis. This last muscle might have caused some long axis rotation if its insertion had spread to the ventral or even posterior surface of the scapula. A small amount of rotation is permitted by the joint and would have the effect of forcing the antebrachium backward. This is important since the powerful triceps muscle could then extend the limb forcing the body forwards. This could have been an important contribution to the otherwise short stride.

The eversion of the acromion process and medial origin of the supracoracoideus are specializations of dicynodonts unknown in the other non-cynodont mammal-like reptiles. As seen, they are already present even in primitive dicynodonts. The advantage of such an arrangement is not immediately obvious. In other reptiles the supracoracoideus and scapulohumeralis attach to the precoracoid and anteroventral part of the scapula. The latter is much more extensive anteroposteriorly than in dicynodonts, and therefore ensures an adequate fibre length of the supracoracoideus. In moving the origin of the muscle on to the medial side of the scapula in dicynodonts, the length of the muscle is not greatly increased since the part of the scapula anterior to the glenoid has been reduced in length. Neither is the direction of the movement produced by the muscle significantly different. The prime selective pressure for development and eversion of the acromion process was probably not then to produce a supracoracoideus which was longer or acted in a different direction. Indeed, there must have been a time immediately before the muscle passed on to the medial side when the anterior part of the scapula had been cut back, producing the incipient acromion process and actually reducing both the area and fibre length of the supracoracoideus.

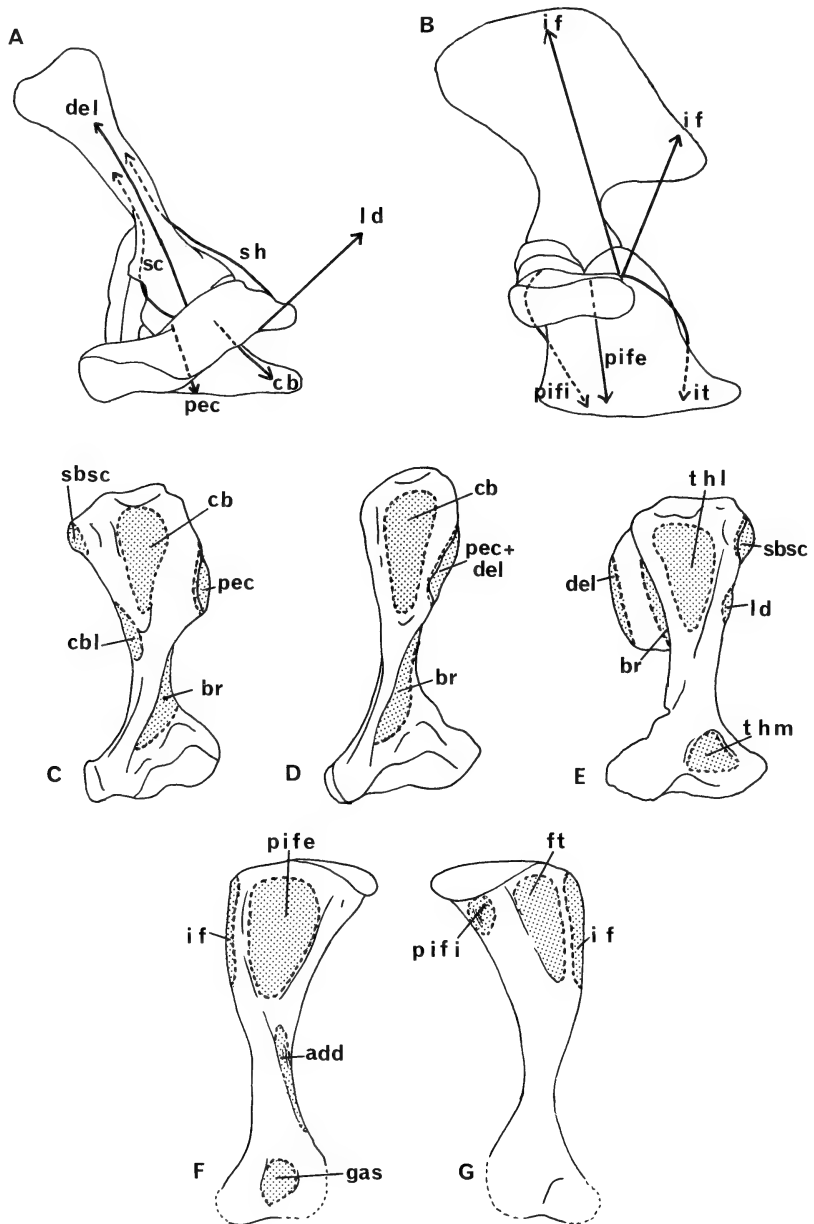


Fig. 7. *Robertia broomiana*, a reconstruction of the pelvic and pectoral musculature. A. The approximate postulated lines of the muscles of the pectoral girdle. B. The approximate postulated lines of the muscles of the pelvic girdle. C-E. Insertions of muscles on the humerus. F-G. Insertions of the muscles on the femur. (In A-B a broken line indicates muscle behind a bone; in C-G a broken outline and stippling indicates the approximate insertional area.)

The acromion process might instead have developed to provide a firmer attachment for the clavicle. However, in the dicynodont shoulder girdle there is less contact between the acromion and the clavicle compared to the pelycosaur condition. Instead the clavicle may be tending to act more as a rod about which the interclavicle and scapula may pivot, rather than a static brace for the girdle. This would seem likely since intra-girdle movements causing rotation of the glenoid may occur in *Dicynodon trigonocephalus* (King 1981). Also, the transition from the pelycosaur screw-shaped glenoid producing a rigidly-defined movement pattern of the humerus (Jenkins 1971) to the open notch-shaped glenoid in therapsids may indicate increased flexibility of the limb. This may be associated with the need for prey capture or traversing uneven terrain or even social behaviour. A less rigid girdle would facilitate such movements as well as possibly increase the stride by allowing a longer excursion of the humerus (King 1981).

In order for the clavicle to act as a rod connecting the interclavicle and scapula, its contacts with them must be reduced to pivoting points. This would initially involve reduction of the anteroventral area of the scapula, leaving the clavicle contact (acromion process) standing proud. At this stage the origin of the supracoracoideus would be diminishing since it cannot extend over the lateral surface of the scapula which is occupied by the deltoideus, and it cannot yet reach the medial surface. At this stage perhaps its role was augmented by the deltoideus and latissimus dorsi. If the acromion process were now everted, for example to increase the length of the clavicle, the supracoracoideus would gain access to the medial side of the scapula, and relieved of the supracoracoideus origin, the anteroventral part of the scapula could be reduced further. It is possible, though, that the supracoracoideus did not play an over-important part in limb movement again, since the latissimus dorsi is probably a more powerful retractor and the deltoideus a better elevator.

HIND LIMB AND PELVIC GIRDLE

The femur (Fig. 8A–B) is a gently S-shaped bone with a distinct shaft. The head is on the anterior margin of the proximal end and is more extensive on the dorsal surface. There is no neck separating the head from the rest of the bone. Ventrally (assuming the femur to be in a position at right angles to the acetabulum) the bone bears a large triangular fossa on its proximal half (Fig. 8A: t fo) which is presumably the insertion of the pubo-ischio-femoralis externus muscle. The anterior boundary of this fossa is a low ridge (Fig. 8A: l r) which bears a rugose striated area just distal to the head (Fig. 8A: r a). This may possibly represent the remains of the internal trochanter seen in pelycosaurs and other therapsids but otherwise absent from dicynodonts. The posterior boundary of the triangular fossa is not as pronounced as the anterior, but a flat ridge (Fig. 8A: f r) is developed which continues on to the shaft of the bone in an anterolateral direction, probably marking the insertion of the ventral adductor muscles. The ridge terminates just proximal to a deep, oval fossa (Fig. 8A: o fo)

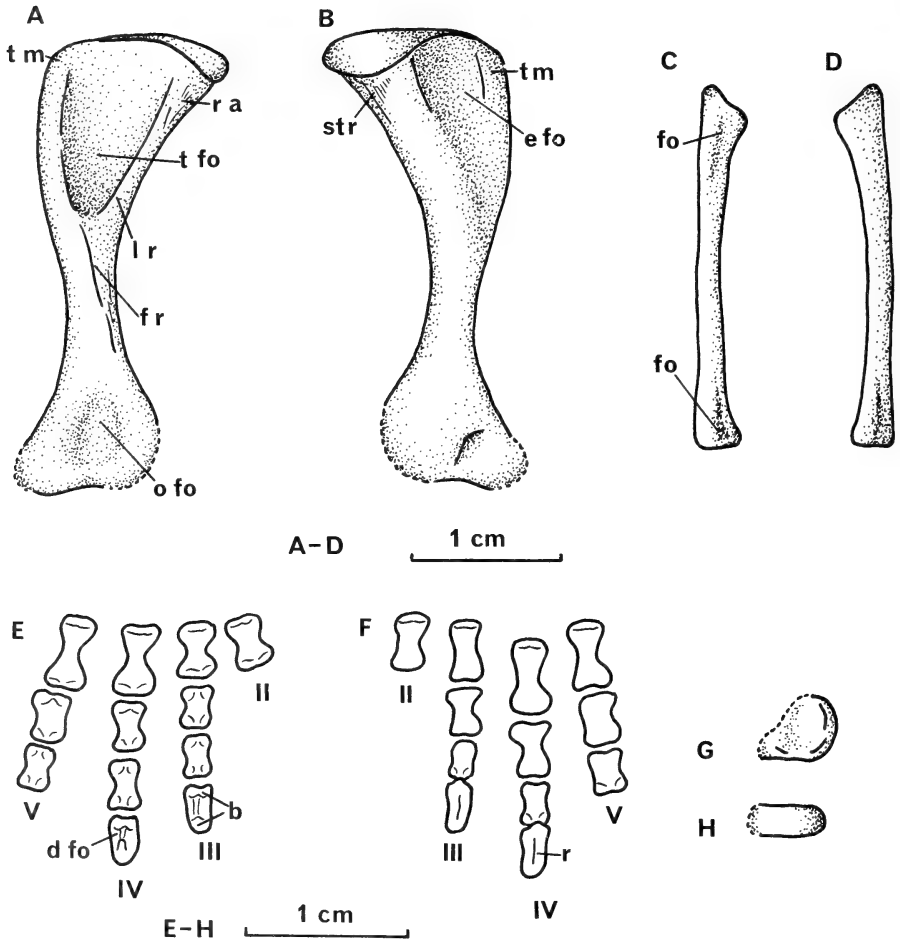


Fig. 8. *Robertia broomiana*, left femur, fibula and hind foot. A. Femur ventral. B. Femur dorsal. C. Fibula posterior. D. Fibula anterior. E. Pes plantar. F. Pes dorsal. G. Tarsal(?) dorsal. H. Tarsal(?) posterior. (Reconstructed from casts 7 and 9.)

occupying the distal part of the ventral surface, indicating the attachment of the gastrocnemius muscle. The trochanter major (Fig. 8A-B: t m) is not at all prominent and is not cut off sharply from the shaft of the bone distally as is the case in *Dicynodon trigonocephalus*. No fourth trochanter is visible.

The dorsal surface of the bone bears a prominent patch of striations (Fig. 8B: str) on its anterior margin just distal to the head. This is a likely insertion for the pubo-ischio-femoralis internus muscle. Posterior to this area the femur is excavated into an elongate fossa which extends well down the bone towards the constricted middle portion (Fig. 8B: e fo). This is probably the extensive origin of the femorotibialis muscle. Posterior to this fossa the edge of the bone is thickened and striated as it is on the ventral surface. Presumably the iliofemor-

alis muscle inserted here, mainly dorsally but also conceivably posteriorly and ventrally.

Only one hind limb epipodial is present. It is identified as the left fibula (Fig. 8C–D). It is a slender bone approximately three-quarters of the length of the femur. The bone is almost straight, the medial edge being only slightly concave. The posterior surface bears two shallow fossae, one in the proximal and the other in the distal half of the bone (Fig. 8C: fo).

Of the pes digits III and IV are complete, V and II are incomplete and I is missing (Fig. 8E–F). Metatarsals II to V are present. One element only of the tarsus is preserved, a small disc-shaped bone (Fig. 8G–H). As in the hand, the metatarsals decrease in size from digit V to digit II. The phalanges decrease in size within a digit distally. The terminal phalanx is a claw, more rounded than that of the hand and bearing a distinct ridge dorsally (Fig. 8E: r). Ventrally the claw bears a boss (Fig. 8F: b) near both its anterior and posterior margins. The area in between is excavated into two small deep fossae (Fig. 8F: d fo).

Most of the ilium is preserved. It is a fan-shaped plate of bone as in most dicynodonts but is expanded anteriorly only to a small degree (Fig. 9). On the anterior margin of the lateral surface it is possible that there is a slight hollowing-out of the bone surface (Fig. 9B: h) distinct from that occupying most of the rest of the lateral surface (Fig. 9B: la fo). The anterior excavation may represent the origin of the iliotibialis muscle, while much of the rest of the bone surface would be occupied by the origin of the iliofemoralis muscle.

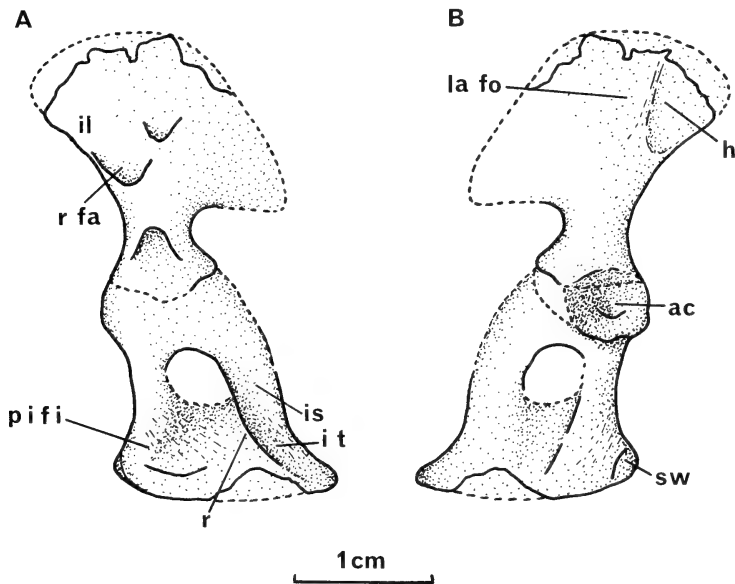


Fig. 9. *Robertia broomiana*, right ilium and pubo-ischiadic plate. A. Medial. B. Lateral. (Reconstructed from casts 7, 8, and 9.)

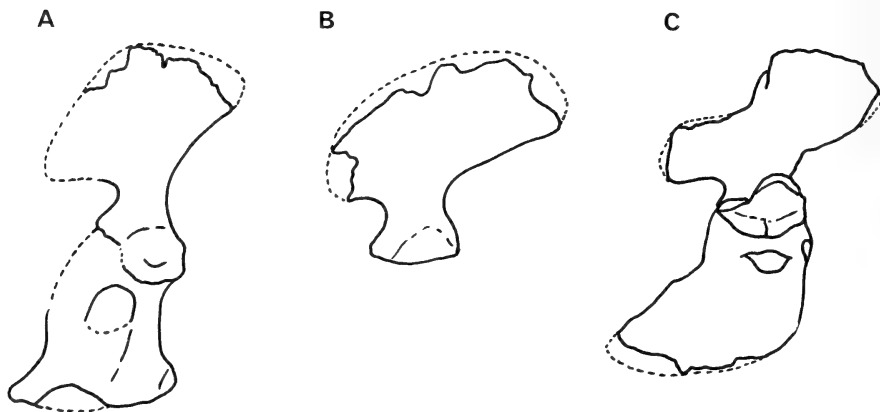


Fig. 10. A comparison of the pelvic girdles of some dicynodonts. A. *Robertia broomiana*. B. T. S. Kemp Collection, Oxford University Museum 83. C. *Dicynodon trigonocephalus*. (B and C reduced to the same width across the ilium-pubo-ischiadic plate symphysis as A.)

The posterior part of the ilium of this specimen is more damaged, but this region of the bone does appear to be quite well developed (Fig. 10).

The medial surface of the ilium shows one clear sacral rib facet (Fig. 9A: r fa). Others are indistinct.

The fused pubis and ischium form a flattish square plate, drawn out into a stout process at its posteroventral corner. The anterior margin is thickened and bears a small swelling (Fig. 9B: sw) ventrally which constitutes the pubic tubercle. More dorsally, the ischiadic contribution to the acetabulum is found. The acetabulum tends to be occluded by the dorsal margin (formed by the ilium) which faces somewhat ventrolaterally. The ventral margin of the acetabulum faces dorsolaterally. The ilium and pubo-ischiadic plate appear to contribute equally to the acetabulum which is situated on the anterior margin of the girdle (Fig. 9B: ac).

A fairly large obturator foramen occupies the middle of the pubo-ischiadic plate. On the medial surface the posterior edge of the foramen is drawn up into a sharp ridge (Fig. 9A: r). Posterior to this ridge is a rugose area, probably the site of the origin of the ischiotrochantericus (Fig. 9A: i-t). Anterior and ventral to the obturator foramen the ventral surface bears a distinct area of striations aligned anterodorsally. This patch of striations does not reach the ventral edge of the plate. It presumably marks the origin of the pubo-ischio-femoralis internus (Fig. 9A: p i f i).

Discussion

As far as can be determined, the femur took up a sprawling position in the acetabulum. The head of the femur is pronounced dorsally and not set off from the rest of the bone at all, and in an erect or even semi-erect position would not contact the articular surface. A very substantial building up of the head in

cartilage would be necessary to achieve this. In a sprawling position the dorsally-facing head comes into contact with the ventrally-facing dorsal margin of the acetabulum. Also, the condyles on the femur for articulation with the tibia and fibula are ventrally-facing, suggesting that the crus was at right angles to the femur, in turn implying that this was perpendicular to the acetabulum.

The muscle configuration of the hind limb (Fig. 7B, F–G) would seem to support this conclusion, since, judging from their areas of attachment, muscles such as the pubo-ischio-femoralis externus, ventral adductor, femorotibialis and gastrocnemius were all well developed. The former two muscles would certainly have had a postural function. The latter two, although concerned with flexing the limb, would also have been important posturally.

However, the position of the head on the anteromedial extremity of the femur does suggest in-turning of the bone implicated in the change from a sprawling to a more erect limb position. If the femur of *Robertia* is compared with that of a pelycosaur such as *Dimetrodon*, however, it can be seen that the head of *Robertia* is not so much in-turned but rather that the posteromedial part of the articular surface has been reduced (Fig. 11). Also, the articular surface of the femur of *Robertia* has become more rounded and bulbous and concentrated on the dorsal side. The obvious consequence of these changes in a sprawling-gaited animal would be to allow a longer protraction–retraction arc before the posterior margin of the femur touched the border of the acetabulum and before contact of the femur head and the acetabulum was lost. In particular,

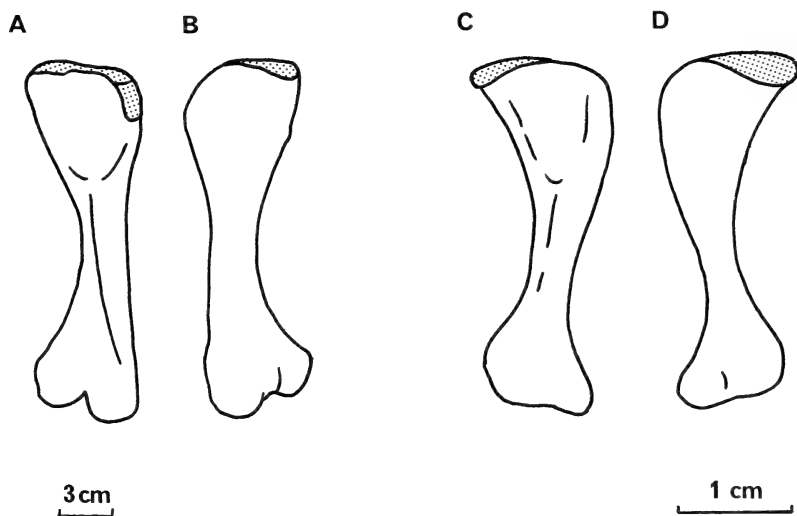


Fig. 11. A comparison of the femora of *Dimetrodon* and *Robertia* reduced to the same approximate length (*Dimetrodon* after Romer 1922). A. *Dimetrodon*, right femur ventral. B. *Dimetrodon*, right femur dorsal. C. *Robertia*, right femur ventral. D. *Robertia*, right femur dorsal. (The articular surface of the proximal end is stippled.)

the positioning of the head on the anterior extremity of the femur allows a great degree of protraction since there is no part of the femur anterior to the head to touch the girdle. Jenkins (1971) notes that in *Dimetrodon* during no part of the stride could the femur be directed more anteriorly than medially because of the shape of the head of the femur. The anterior position of the head in *Robertia* can, therefore, be seen as an adaptation to extensive protraction as a way of lengthening the stride.

However, although retaining a sprawling gait, there is no sign in *Robertia* of a powerful caudifemoralis acting as a retractor. Instead the iliofemoralis must have had this role. With the femur in a sprawling position the iliofemoralis can act as a retractor only if its origin is on the posterior part of the ilium. If its origin is more anterior, then the insertion must be posterior to the point of rotation of the femur in the acetabulum, that is, on a pronounced trochanter major. In *Robertia* there is no such pronounced trochanter major, so even a far anterior origin would not allow the iliofemoralis to act as a retractor, and, in fact, it is seen that the ilium is not expanded far anteriorly, and quite possibly the anterior margin was occupied by the iliotibialis in any case. In *Robertia* probably the farthest anterior that the iliofemoralis fibres insert is over the acetabulum. These fibres would only retract the femur from a midstride position. When the femur was fully protracted, posteriorly-originating fibres would be necessary to initiate retraction. The posterior extension of the ilium was, therefore, necessary to provide adequate origin for this part of the iliofemoralis.

However, this does not explain why the iliofemoralis took over from the caudifemoralis as a retractor muscle. Possibly as the excursion of the femur became greater, especially the point to which it could be protracted, then the fibres of the caudifemoralis might have been too short to allow the increased degree of protraction. This problem does not face the iliofemoralis, since, whether the limb is protracted or retracted, the length between the origin and insertion of the iliofemoralis does not change a great deal because its origin is above the femur rather than far posterior to it.

If the iliofemoralis, by gaining a more posterior insertion on the femur, could function equally well as the caudifemoralis as a retractor, then the further evolution of the iliofemoralis may be favoured for another reason. If the insertion migrated on to the posterior edge of the femur, or better still, on to the ventral margin of the posterior edge, then the muscle could also cause long axis rotation. This would be in an anti-clockwise direction on the left-hand side, forcing the crus backwards. The powerful extensor muscles (femorotibialis) could then extend the limb, imparting a forward thrust to the body. This would be a significant contribution to the overall locomotory thrust developed.

This development of long axis rotation might have been very important since, in later dicynodonts when a larger trochanter major is developed, retraction becomes more limited because the trochanter touches the acetabulum. However, by this time long axis rotation is well established in the limb movement and contributes greatly to the stride.

The above arguments imply that reduction of the length of the tail occurred concomitantly with the reorganization of the iliofemoralis muscle and was a rather passive process: as the iliofemoralis became the main retractor muscle, the caudifemoralis was no longer needed and therefore its origin (the caudal vertebrae) could be reduced. However, an alternative view, that reduction of the tail was actively selected for and that reorganization of the iliofemoralis followed as a consequence of this, is also possible. In this case one would need to postulate a selective pressure for tail-shortening. Geist (1972) suggests that tail-shortening would be favoured in therapsids that lived in cool environments as a means of reducing heat loss. A shorter tail and other appendages would help the animal to approximate to a sphere, giving the most advantageous surface area : volume ratio. Geist argues that having reduced heat loss, such therapsids could maintain a fairly high body temperature without the need to consume vast quantities of food. To be most successful these adaptations would be coupled to large size, and Geist cites *Kannemeyeria* as an example of such a homeotherm.

Geist attempts to demonstrate the change in surface area brought about in a hypothetical animal when the length of its tail is reduced by half, keeping the total mass of the body constant. A similar exercise can be carried out with *Robertia*, first allowing a tail 10 cm long (which is approximately two-thirds body length) and then allowing a tail length of 4 cm (which is the approximate actual length of the tail). The surface area: volume ratios obtained are very approximate since Geist's method reduces the form of the animal to a right regular conical head, a cylindrical body, and a conical tail. The ratios obtained for *Robertia* are, with the long tail 0.775, and with the short (actual) tail 0.665. The change in the ratio is 14.21 per cent. This is obviously a substantial change and would be significant to the animal's temperature control system. However, to achieve this the volume of the tail (presumably mostly muscle) has been reduced by 80 per cent. It is difficult to envisage such a reduction occurring in one evolutionary event since it will have great repercussions on the reptilian mode of locomotion. However, if the reduction occurred gradually, it is difficult to see the advantage in terms of thermoregulation that the incipient stages would bring. In conclusion, then, although tail reduction may benefit an animal by reducing its surface area once a short tail was fully evolved, it is difficult to imagine this as a prime selective pressure.

It is possible, instead, to visualize tail reduction as part of a suite of characters which enable an animal to become more manoeuvrable during locomotion, as discussed in connection with the forelimb. This increased manoeuvrability may not only be advantageous at high speeds, but also at low speeds over uneven terrain. It would then assume great importance for small animals to whom even small discontinuities in the terrain pose large problems of manoeuvrability.

One stage in producing this manoeuvrability would be reduction of lateral undulation in the locomotory pattern. Although *Robertia* still seems to retain

the possibility of lateral flexibility (see page 226), later dicynodonts such as *Dicynodon trigonocephalus* (King 1981) do not. Kemp (1980) has indicated the possible advantages of an animal possessing a rigid vertebral column:

1. During fast locomotion, momentum would be maintained if the animal followed a linear path. Lateral deviation from this path by parts of the body would cause a loss of momentum.

2. If the hind limb produces most of the significant locomotory thrust, then the whole of the locomotory forces applied to the animal pass forward along the spinal column. Any slight distortion of the vertebral column then leads to a large bending moment, tending to cause collapse of the animal between fore and hind limbs.

It has been shown earlier (page 213) that most of the muscles of the pectoral girdle in *Robertia* had a postural function and it is possible, therefore, that the forelimb produced a much weaker locomotory thrust than the hind limb. Both of the advantages listed above might then have applied to *Robertia*. Furthermore, during lateral undulation the head would be moving continually from side to side. This may be a grave disadvantage for an animal feeding on small invertebrates which it may need to catch while running. Both Cruickshank (1980 pers. comm.) and Cluver (1978) have suggested that small dicynodonts might have included terrestrial invertebrates in their diet, and therefore the ability to both sight and catch prey effectively might have been a factor in keeping the path of the head as straight as possible during locomotion.

Manoeuvrable animals sacrifice some stability for agility. Instead of relying on body proportions and size for stability, they tend to rely on postural changes brought about by neuromuscular control to counteract overbalancing forces. If a loose inverse relationship between stability and manoeuvrability is assumed, then it is possible that loss or reduction of a tail may increase manoeuvrability by decreasing stability. The tail could act as a stabilizing organ in the following way: an animal relying on lateral undulation in its locomotory pattern faces a problem of instability; as the animal flexes its body the limb on the convex side of the flexure will be off the ground, in the act of completing the recovery stroke; because of the body flexure the triangle formed by the other three anchored legs may be so placed that there is a possibility of the animal's centre of gravity falling outside the triangle; it would, therefore, tend to collapse in the direction of the unanchored leg; this tendency could be counteracted by a fairly massive tail flexed in the same direction as the head, that is, away from the unanchored leg. Now, if the possibility of lateral undulation is lost, as in the later dicynodonts, then the tail is not needed as a balancing organ. In fact, if increased manoeuvrability is being selected, then a large tail with a large moment of inertia is actually undesirable.

A third stage in increasing manoeuvrability would be to accentuate the problem of instability outlined above by decreasing the triangular area formed by the anchored leg. One way of doing this is by altering the stance of the animal from a sprawling mode to one where the legs are pulled in underneath

the body. At the expense of stability the animal can bank and turn rapidly if necessary.

There is probably no fixed order in which these stages should appear in therapsid evolution. They must to some extent appear together. In *Robertia* lateral undulation has not been eliminated nor are the legs turned in under the body, but the tail is shortened. In later dicynodonts such as *Dicynodon trigonocephalus*, the tail is short, lateral undulation has been reduced and the hind limbs are pulled in somewhat. Such a suite of characters may be widespread in the mammal-like reptiles.

AXIAL SKELETON

Various sequences of vertebrae and ribs are present in the specimens. None is complete from neck to tail, however, so the total number of vertebrae in the column is uncertain. The pre-sacral number is probably approximately twenty-six. Two sacral vertebrae are preserved and eleven caudal.

The atlas and axis vertebrae are damaged but appear to have the same forms as that described in *Dicynodon trigonocephalus* (King 1981). The neck vertebrae following (Fig. 12A) have slightly shorter neural spines than subsequent vertebrae and show the distinctive facets for the double-headed ribs (Fig. 12A: r fa), one on the centrum and the other on the transverse process. Proceeding from vertebra 4 to vertebra 7, it is seen that the centrum facet gradually increases in area and migrates dorsally on the centrum. Gradually the transverse process facet is lost, the sole articulatory facet being the elongate centrum facet as on vertebra 15 (Fig. 12B). The point at which the two heads of the rib coalesce is not known in this case. It is usually about vertebra 9 or 10. As in other dicynodont specimens, the ribs of vertebra 8 and 9 are particularly robust and bear a pronounced fossa on the midline of the posterior surface (Fig. 13D: p fo). The fossa between the two heads on the posterior surface is also very pronounced (Fig. 13D: h fo).

In the posterior dorsal vertebrae the rib facet begins to decrease in area, and migrates upwards towards the transverse process (Fig. 12C: r fa). The ribs associated with these vertebrae are also much less robust. After the particularly robust ribs of the shoulder region, there is a trend towards lighter but long ribs in the dorsal region (Fig. 13E). However, these begin to decrease in length at about vertebra 21 and are much reduced by vertebra 26 (Fig. 13F).

Several of the mid-dorsal and thoracic ribs are complete, though broken. Viewed posteriorly or anteriorly, the rib is a smooth arc of a circle of very long radius. There is no sudden change in the radius of curvature. Viewed dorsally, the ribs have a distinct backward as well as downward curvature. Because the ribs of the thoracic and lumbar regions of the spinal column are so long (almost twice the length of the epipodial) and rather straight, they must have been orientated backward in the body at a considerable angle (Fig. 15). Even so, the thorax and abdomen were probably only just clear of the ground in the normal stance. The cross-section of the thorax would have been almost circular.

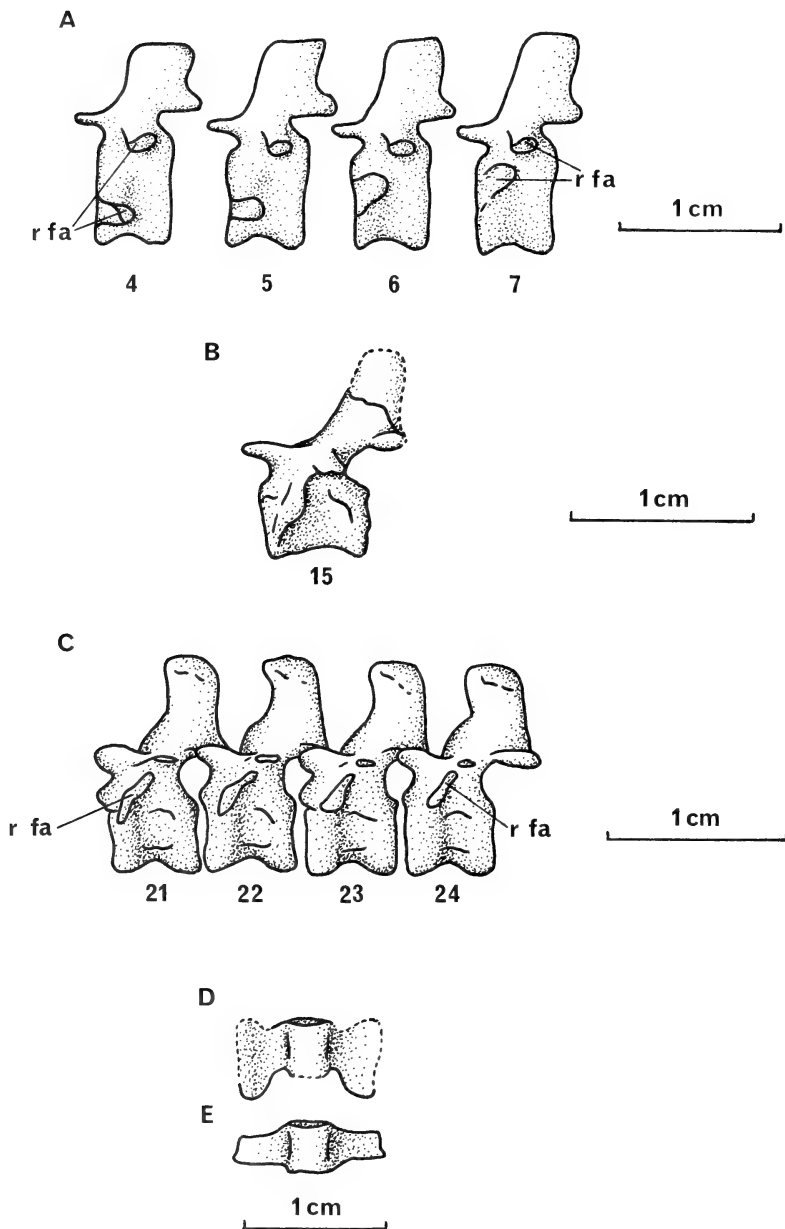


Fig. 12. *Robertia broomiana*, vertebrae. A. Vertebrae 4 to 7 lateral. B. Vertebra 15 lateral. C. Vertebrae 21 to 24 lateral. D. Second? sacral vertebra ventral. E. Third? sacral vertebra ventral. (A reconstructed from cast 5; B reconstructed from cast 6; C reconstructed from cast 8; D-E reconstructed from cast 7.)

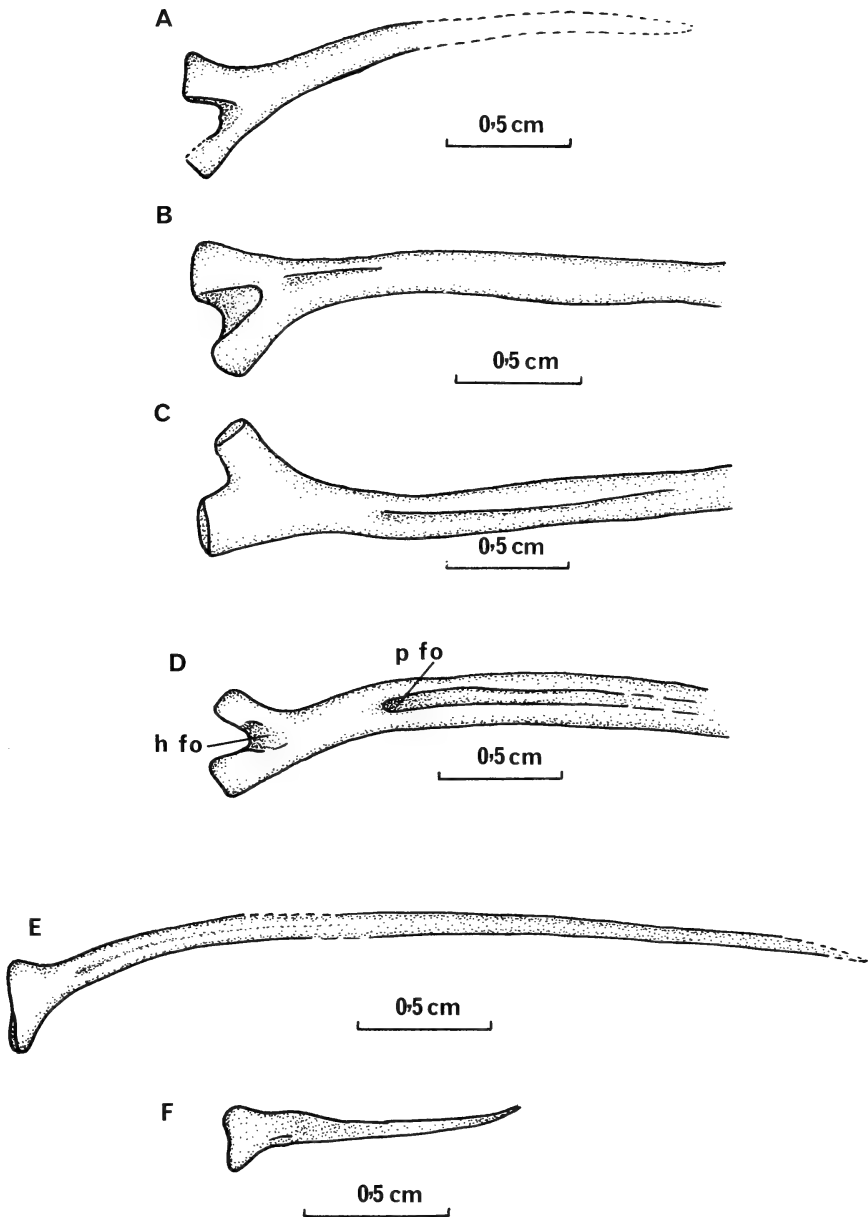


Fig. 13. *Robertia broomiana*, ribs. A. Rib 2 or 3 posterior. B. Rib (probably 6) posterior. C. Rib (probably 6) anterior. D. Rib (probably 8) posterior. E. Mid-dorsal rib anterior. F. Last presacral rib anterior. (A–C reconstructed from cast 5; D reconstructed from cast 3; E reconstructed from cast 6; F reconstructed from cast 8.)

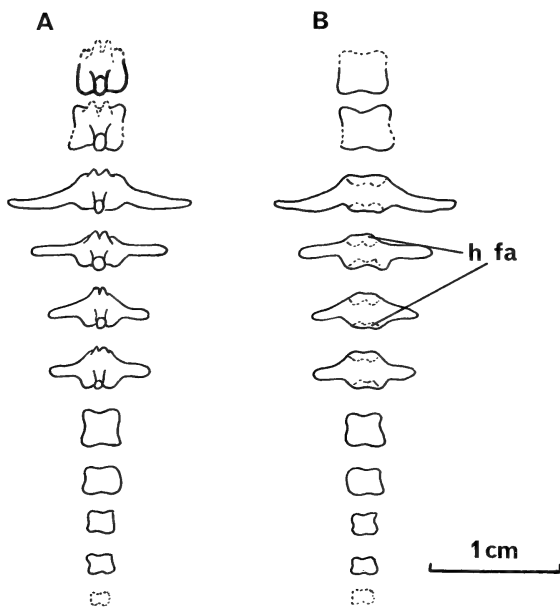


Fig. 14. *Robertia broomiana*, caudal vertebrae. A. Dorsal. B. Ventral. (Reconstructed from casts 7 and 9.)

The zygapophyses of the pre-sacral vertebrae do not show much morphological change along the column. The anterior zygapophyses tend to be shallow and wide, forming articulations with the posterior zygapophyses which are almost horizontal. Presumably these allowed extensive side-to-side movements of the vertebrae, so that in a horizontal plane the vertebral column was very flexible. This flexibility and the long, slender body must have made *Robertia* appear quite lizard-like. The limb proportions of a small lizard such as *Lacerta ocellata* are also similar to *Robertia*'s including the slightly longer dimensions of the hind limb compared to the forelimb. Unlike *Lacerta*, however, the forelimb of *Robertia* is very robust.

The neural spines of the pre-sacral vertebrae do not slope backward to any great degree and are quite short, being less than the height of the centrum.

Two sacral vertebrae are preserved but presumably more were present in life (Fig. 12D–E). It does not seem likely that more than three were present in life though, judging from the length of the ilium and the length of the sacral ribs. Of the two vertebrae preserved, the ribs are much more expanded on the anterior, and it is possible that they represent the second and third sacral vertebrae, respectively.

The tail is reasonably well preserved (Fig. 14). The first two caudal vertebrae have no ribs attached to them. The next four vertebrae have fused ribs which gradually diminish in size along the column. Traces of haemal arch facets (Fig. 14B: h fa) can be seen on these vertebrae. The last five vertebrae are

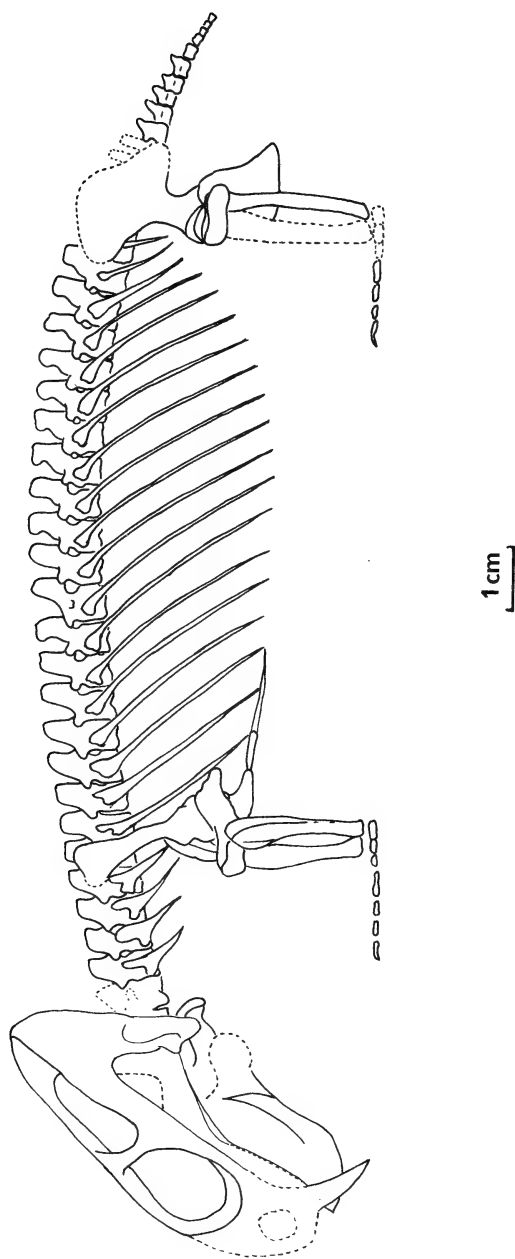


Fig. 15. *Roberitia broomiana*, a reconstruction of the entire skeleton.

cuboids of bone with few distinguishing features preserved. The tail is thus short, approximately one-eighth body length, and, judging from the limited area for muscle attachment, also lightly built.

SUMMARY AND CONCLUSIONS

The postcranial skeleton of *Robertia broomiana* shows a mixture of advanced and primitive characters which may be expected of an early (*Tapinocephalus* zone) dicynodont. The specialized characters of dicynodonts include the production and eversion of the acromion process; the reduction of the pre-glenoid area of the scapula; the medial origin of the supracoracoideus muscle; the posterior and anterior extension of the ilium; the reduced caudifemoralis muscle and the role of the iliofemoralis as the limb retractor; reduction of the fourth trochanter; absence of an internal trochanter; anterior position of the head of the femur; the short tail; the large thorax and abdomen; and the digital formula. Many of these characters are as fully developed in *Robertia* as they are in much later dicynodonts. The lack of elaboration of the iliofemoralis is an exception to this.

Features of *Robertia* which appear to be primitive for therapsids generally include the sprawling position of the forelimb; extensive postural musculature and musculature associated with forelimb extension; the remnant of an ectepicondylar foramen; the small trochanter major; the small extension of the anterior edge of the ilium; large hind limb postural muscles; the small number of sacral ribs; the sprawling position of the femur; the flexible spine.

Robertia was a small, probably rather active animal, a little like modern lizards. Although an analysis of the skull is necessary before any conclusions can be drawn, it is not impossible that *Robertia* not only fed on softer plant matter but also on small invertebrates, when the teeth may have played a part in food capture or processing

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It is a pleasure to thank Dr M. A. Cluver of the South African Museum not only for providing the specimens but also for much stimulating discussion about them. Mr Neville Eden of the same Museum made the excellent casts of the material for which I am very grateful. My thanks are also offered to Dr T. S. Kemp for useful discussion of the manuscript and specimens.

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ABBREVIATIONS

ac	acetabulum
ac p	acromion process
add	adductor muscles
b	boss
br	brachialis muscles
cb	coracobrachialis muscle
cb l	coracobrachialis longus muscle
ce?	possible centrale
c fa	coracoid facet of the glenoid
cl	clavicle
cor	coracoid
d	dentary
d e	distal end of the clavicle
del	deltoideus muscles
d fo	deep fossa
d p c	deltopectoral crest
d s	dentary shelf
ect f	extepicondylar foramen
e fo	elongate fossa
ent f	entepicondylar foramen
fo	fossa
f r	flat ridge
ft	femorotibialis muscle

gas	gastrocnemius muscle
gl fa	scapula facet of the glenoid
h	hollowing out of the ilium
hd	head
h fa	haemal arch facet
h fo	fossa between the heads of a rib
ic	interclavicle
if	iliofemoralis muscle
il	ilium
int	intermedium
is	ischium
i-t	origin of the ischiotrochantericus muscle
la fo	fossa on the lateral surface of the ilium
l d	attachment of the latissimus dorsi muscle
l r	low ridge
m fo	marked fossa
m r	medial ridge
mx	maxilla
n	notch
o fo	oval fossa
o p	olecranon process
p	parietal
pal	palatine
pc	precoracoid
pec	pectoralis muscles
p fo	fossa on the posterior surface of a rib
pi	pisiform
p i f e	pubo-ischio-femoralis externus muscle
p i f i	pubo-ischio-femoralis internus muscle
pmx	premaxilla
pof	postfrontal
pp	preparietal
pr fo	proximal fossa
pro	protuberance
pt	pterygoid
pu	pubis
q	quadrate
rad	radius
r	ridge
ra	radiale
r a	rugose area
rad fa	radial facet on the humerus
r fa	rib facet
r fo	rugose fossa
sbsc	subscapularis muscle
sca	scapula
sc	supracoracoideus muscle
s fo	shallow fossa
s h	scapulohumeralis muscle
sm sw	small swelling
sq	squamosal
s r	short ridge
str	striations
sw	swelling
t	teeth
t fo	triangular fossa
t h l	triceps humeralis lateralis muscle
t h m	triceps humeralis medialis muscle
t m	trochanter major

tr	trough
tub	tubercle
u	ulna
ul fa	ulnar facet on the humerus
v	vertebra
v s	ventral surface of the deltopectoral crest
I-V	digit numbers

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family *Nuculanidae*

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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- The Figures, Maps and Tables of the paper when referred to in the text
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- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
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e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

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'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

G. M. KING

THE POSTCRANIAL SKELETON OF
ROBERTIA BROOMIANA, AN EARLY
DICYNODONT (REPTILIA, THERAPSIDA)
FROM THE SOUTH AFRICAN KAROO

84 PART 6

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(continued inside back cover)

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UNGULATE MORTALITY AND SEDIMENTARY
FACIES IN THE LATE TERTIARY
VARSWATER FORMATION, LANGEBAANWEG,
SOUTH AFRICA

By

R. G. KLEIN

Cape Town Kaapstad

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UNGULATE MORTALITY AND SEDIMENTARY FACIES IN THE LATE TERTIARY VARSWATER FORMATION, LANGEBAANWEG, SOUTH AFRICA

By

RICHARD G. KLEIN

Department of Anthropology, University of Chicago

(With 7 figures and 3 tables)

[MS. accepted 15 January 1981]

ABSTRACT

Dental crown heights are used to establish mortality profiles for the giraffids *Sivatherium hendeyi* and *Giraffa* sp., the bovids *Mesembriportax acrae* and *Simatherium demissum*, and the rhinoceros *Ceratotherium praecox* from the early Pliocene Varswater Formation. The giraffid mortality profiles exhibit classic 'catastrophic' shapes, in which progressively older age classes contain progressively fewer individuals, similar to the age structure of a live population of large mammals. This suggests that the giraffids died from a cause that does not select with respect to age. Since the giraffid remains come from an ancient river channel, the most probable cause is drowning during flood periods. Giraffid bones far outnumber those of other species in the channel fill, suggesting that the giraffids were particularly prone to drowning, probably because their feeding habits tied them to the proximity of the river even during flood intervals. The mortality profiles of the other species all exhibit 'attritional' shapes, in which prime-age adults are seriously under-represented relative to their probable live abundance. For the rhinoceros and a portion of the *M. acrae* individuals, the remains of which accumulated subaerially on the estuarine floodplain adjacent to the river channel, the implication is that death was due mainly to predation, accidents, endemic disease, and other mortality factors that disproportionately affect the very young and the old. For the remainder of the *M. acrae* individuals and for *S. demissum*, the remains of which came from the same channel fill as the giraffid bones, it seems likely that death by attritional causes was followed by secondary incorporation of bones in the river channel.

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THE LANGEBAANWEG FOSSIL SITE

The occurrence of vertebrate fossils exposed by open-cast phosphate mining at Langebaanweg (18°9'E 32°58'S) (Fig. 1) was first reported in 1958 (Singer & Hooijer 1958; Singer 1961). Research since then, supervised mainly by Q. B. Hendey of the South African Museum, has led to a vast accumulation of specimens, making Langebaanweg one of the most prolific sources, if not the

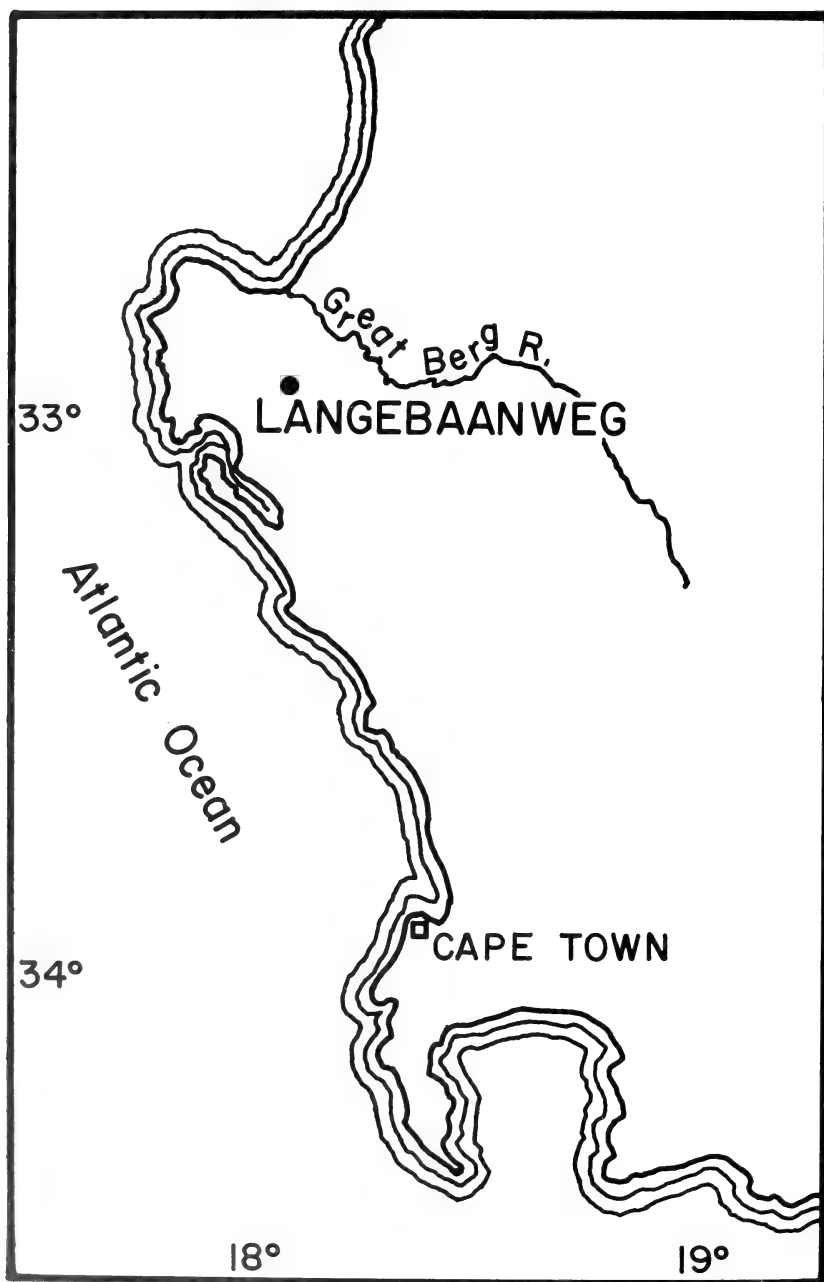


Fig. 1. The approximate location of Langebaanweg.

most prolific source, of late Tertiary vertebrate fossils anywhere in the world. Henzey (1970a, 1970b, 1972a, 1973, 1974, 1976a, 1981; Henzey & Deacon 1977) has published periodic overviews of the site, as well as descriptions and analyses of the carnivore taxa represented in the deposits (Henzey 1972b, 1974, 1977, 1978a, 1978b, 1980; Henzey & Repenning 1972; De Muizon & Henzey 1980). Specialist reports have also appeared on the invertebrates (Kensley 1972, 1977; Tankard 1975), penguins (Spheniscidae) (G. Simpson 1971, 1975, 1979), other birds (Rich 1980), micromammals (Pocock 1976), proboscideans (Maglio & Henzey 1970; Maglio 1973: 51 ff.), perissodactyls (Boné & Singer 1965; Hooijer 1972, 1976), peccary (Tayassuidae) (Henzey 1976b), giraffids (Harris 1976), and bovids (Gentry 1974, 1980).

By far the most important source of fossils at Langebaanweg has been the open-cast phosphate mine known as the New Varswater Quarry or, more informally, as 'E' Quarry, whose sedimentary sequence has been discussed by Bishop (1980), Butzer (1973), Dingle *et al.* (1979), and Henzey (various review papers cited above, especially 1981). The lowermost unit exposed in 'E' Quarry consists of phosphatic pebbles and cobbles in an unconsolidated sand matrix. Both invertebrate and vertebrate fossils are relatively abundant, while marine taxa predominate very heavily. The deposit is clearly of marine origin and was formed when the Atlantic coast, presently located 13 km to the west, intersected the area exposed by the quarry.

Nonconformably overlying the marine unit are the deposits which have provided the vast majority of terrestrial fossils from 'E' Quarry, including all those discussed here. These deposits, assigned to the Varswater Formation, comprise two principal units, referred to by Henzey as the Quartzose Sand Member (older) and Pelletal Phosphorite Member (younger).

The Quartzose Sand Member (QSM) consists primarily of fine-grained, non-phosphatic, white quartz sands reaching a thickness of up to 2 m. Lateral gradation into salt marsh and tidal mudflat sediments indicates that the sands were laid down on the estuarine floodplain of a river that probably entered the sea to the south-west of 'E' Quarry. The sands and associated facies contain both vertebrate and invertebrate fossils, but terrestrial vertebrates predominate. Abraded bones are rare, while partial, semi-articulated skeletons are common. Post-mortem fluvial disturbance of skeletons is believed to be minimal; scavengers and other biological agents were probably responsible for most bone disarticulation, displacement, and destruction.

The Pelletal Phosphorite Member (PPM) consists of up to 20 m of relatively coarse, generally well-sorted sands incorporating a variable quantity of phosphate pellets. Commercial exploitation centres on these deposits. Fossils are sparse through much of the deposit, but very substantial concentrations occur in the subunits named Beds 3aS and 3aN, which represent successively more northerly channel fills of the same river that was responsible for deposition of the Quartzose Sand Member. Vertebrate fossils predominate heavily, and terrestrial forms are best represented. In contrast to the situation in the QSM, in

the PPM abraded bones are common, and partial, semi-articulated skeletons are virtually unknown. The majority of bones are believed to have been deposited by the ancient river on bars within its channel.

There are no materials suitable for radiometric age determination at Langebaanweg, but it is possible to estimate the age of the deposits by comparing the taxa they contain to taxa found in dated contexts elsewhere (especially in east Africa) and by a consideration of the global sea-level and climatic events that are reflected in the Langebaanweg geologic sequence. On this basis, Hendey (1981) has concluded that the marine unit at the base of the sequence is probably of middle to late Miocene age, while the QSM and PPM are probably about 5 million years old, or early Pliocene as the term is presently defined.

The river, which was primarily responsible for the deposition of the QSM and PPM sediments, was almost certainly the precursor of the modern Great Berg, which now flows into the sea 20 km north of Langebaanweg from an origin in the mountains of the south-western Cape 70 km and more to the east (Fig. 1). In a broad sense, the channel and estuarine floodplain of the Great Berg provide analogues for the depositional environment of the QSM and PPM, although the QSM and PPM fossil assemblages point to a very different climatic and biotic setting than the historic one. Perhaps most striking is the presence of giraffids, which are particularly abundant in the PPM. Giraffids were totally absent in the historic fauna of the region, reflecting the historic absence of suitable browse trees. Tree growth in early Pliocene times was probably promoted by higher annual rainfall (the historic average near Langebaanweg is about 250 mm/a), perhaps combined with a different seasonal distribution of rainfall (presently confined almost entirely to the winter months). Greater rainfall may be more directly inferred from the QSM and PPM sediments, which indicate that the ancient river carried substantially more water than the historic Great Berg, at least seasonally.

Although essentially the same mammalian taxa are represented in both the QSM and the PPM, their relative abundance varies dramatically between the two units. Generally speaking, there is a tendency for several species to be subequally represented in the QSM, with no single species dominating overwhelmingly. In contrast, in the PPM, alcelaphine antelopes (*Damalacra* spp) and giraffids (*Giraffa* sp. and especially *Sivatherium hendeyi*) are superabundant v. other species. Within the PPM, alcelaphines dominate heavily in Bed 3aS and giraffids in 3aN. Since Beds 3aS and 3aN were deposited under similar circumstances—both are primarily channel fills of the proto-Great Berg—the difference in their fossil contents may reflect vegetational change, from more open vegetation in 3aS (dominated by grazing alcelaphines) to more closed (wooded) vegetation in 3aN (dominated by browsing giraffids). Vegetational change may also account for the superabundance of alcelaphines and giraffids in the PPM v. the QSM, but it seems equally possible that the alcelaphines and giraffids are so common because they were much more likely to drown than other species and thus had a far higher probability of becoming incorporated in channel sediments.

The implication would probably be that the alcelaphines and giraffids were more inclined than other species to remain near the river for feeding (?the giraffids) or to attempt crossings (?the alcelaphines) during periods of (?seasonally) high flow.

Flooding as a cause of death tends to select its victims without regard for age. Therefore, if the alcelaphines and giraffids are superabundant in the Bed 3aS and 3aN channel fills, at least in part because these species were especially prone to drowning during flood periods, analysis of their remains may be expected to produce age (= mortality) profiles in which the age structure of the original live populations is closely mirrored. In contrast, if animals represented in the QSM died primarily from predation, endemic disease, accidents, etc. on the ancient floodplain, analysis of their remains should produce age profiles in which those classes most prone to death by predation, etc.—the very young and the old—are disproportionately well represented compared to their initial live abundance. Mortality profiles reflecting death from an agency such as flooding that is non-selective with respect to age are sometimes called 'catastrophic', while profiles reflecting death from predation, accidents, endemic disease, and other causes that disproportionately affect the very young and the old are sometimes called 'attritional' (Voorhies 1969, with references).

This paper presents mortality profiles for some pertinent QSM and PPM ungulate species in order to help determine whether differences in relative taxonomic abundance between the units reflect vegetational change or the difference in depositional facies. More generally, the mortality profiles are obviously relevant for reconstructing the ancient Langebaanweg environment, as well as the behaviour of its inhabitants. Finally, the profiles may be compared to those from other sites, for example those where bones were accumulated by people, to help explain the nature of ungulate mortality there.

MATERIALS AND METHODS FOR CONSTRUCTING AGE (= MORTALITY) PROFILES

In general, teeth monitor advancing age more closely than any other element in mammals. At Langebaanweg, as in most fossil assemblages, they are also among the easiest elements to identify taxonomically, and they are also relatively abundant because of their durability. These are the reasons that teeth were chosen to construct age profiles for various QSM and PPM taxa.

The taxa to be analysed were selected partly for their absolute abundance in the QSM or the PPM and partly for their suitability to age determination by the method discussed below. The rhinoceros, *Ceratotherium praecox*, and the boselaphine antelope, *Mesembriportax acrae*, were the most suitable species in the QSM, while the giraffids, *Sivatherium hendeyi* and *Giraffa* sp., the buffalo, *Simatherium demissum*, and the boselaphine, *M. acrae*, all as represented in Bed 3aN, were the most suitable examples in the PPM.

The *Giraffa* sample almost certainly includes some teeth from the dentally very similar *Palaeotragus* cf. *germaini*, an okapi-like giraffid represented by

ossicones in Bed 3aN. However, the relative rarity of the ossicones, combined with the homogeneity of the *Giraffa* dental samples, as reflected in relatively small coefficients of variation (Table 1), suggests that 'contamination' by *Palaeotragus* is probably very limited.

A more serious possibility of taxonomic mixture exists in the Bed 3aN boselaphine sample, in which the coefficients of variation are very large (Table 1), confirming a visual impression of substantial size variability. On average, the Bed 3aN boselaphine teeth are significantly larger than their QSM counterparts (Fig. 6 and Table 1), and it is possible that the 3aN sample reflects a rapid trend

TABLE 1

Sample size (N), mean (\bar{x}), standard deviation (s), and coefficient of variation ($V = 100s/\bar{x}$) for measurements of basal breadth and unworn crown height on selected teeth of *Ceratotherium praecox*, *Sivatherium hendeyi*, *Giraffa* sp., *Simatherium demissum*, and *Mesembriportax acrae* in the Quartzose Sand Member and Bed 3aN of the Pelletal Phosphorite Member, 'E' Quarry, Langebaanweg. The measurements are defined in Figures 2 to 6 and presented in millimetres. G. Simpson *et al.* (1960) suggest that biologically homogeneous samples generally exhibit coefficients of variation that are less than 10. A coefficient of more than 10 may indicate that a sample includes specimens from more than one species. The data presented below suggest that species admixture may be a problem with respect to the sample attributed to *Mesembriportax acrae* in Bed 3aN.

	dP ⁴				P ⁴			
	N	\bar{x}	s	V	N	\bar{x}	s	V
<i>Ceratotherium praecox</i> (QSM)								
basal breadth	10	55,65	2,34	4,13	43	70,32	3,46	4,92
unworn crown height	—	—	—	—	1	65,1	—	—
	dP ₄				M ₃			
	N	\bar{x}	s	V	N	\bar{x}	s	V
<i>Sivatherium hendeyi</i> (3aN)								
basal breadth	324	20,45	1,52	7,43	153	33,98	1,79	5,27
unworn crown height	—	—	—	—	42	42,78	2,28	5,33
<i>Giraffa</i> sp. (3aN)								
basal breadth	51	14,93	1,26	8,44	46	34,88	1,37	5,51
unworn crown height	4	15,08	1,26	8,36	10	27,02	0,73	2,70
<i>Simatherium demissum</i> (3aN)								
basal breadth	2	12,75	1,06	8,31	15	19,05	1,30	6,82
unworn crown height	—	—	—	—	—	—	—	—
<i>Mesembriportax acrae</i> (QSM)								
basal breadth	7	9,40	0,58	6,17	17	15,18	1,09	7,18
unworn crown height	—	—	—	—	—	—	—	—
<i>Mesembriportax acrae</i> (3aN)								
basal breadth	4	10,18	0,98	9,63	21	17,05	2,77	16,25
unworn crown height	—	—	—	—	1	27,2	—	—

towards increasing size in *Mesembriportax acrae* in 3aN times, or a mixture of specimens from *M. acrae* and a larger (unidentified) boselaphine, or from *M. acrae* and a larger, dentally very similar tragelaphine. Sorting out the alternatives remains a goal of future research. For the moment, the possibility of sample mixture limits, but does not entirely rule out, interpretation of the Bed 3aN boselaphine age profile.

The two alcelaphine antelope species (*Damalacra neanica* and *D. acalla*), that are superabundant in Bed 3aS and that are perhaps the best represented species in the composite Langebaanweg assemblage, were excluded from consideration because criteria to separate their teeth have not yet been developed. A search for such criteria is planned, and if none are found, a mortality profile based on mixed samples will be presented in a future paper. Future research should also permit the presentation of profiles for several additional ungulate species represented in the QSM, the PPM, or both, and perhaps also for some well-represented carnivores.

In theory, at least three basic methods exist for estimating individual age from teeth (see Morris 1972 or Spinage 1973 for general reviews). The first involves counting the number of growth increments or 'annuli' in cementum on the roots of teeth. In many species, including close living relatives of some that are important here, annuli counts have been shown to correlate closely with age. A more obvious, but generally less accurate method of age determination is subjective evaluation of dental eruption and wear. Finally, age may be estimated by measuring a dental dimension, particularly crown height, that clearly varies with age.

Cementum annuli are often difficult to observe and count in fossils (Spiess 1979), and the preparation of teeth for examination is time-consuming and destructive. Subjective evaluation of dental eruption and wear generally results in age classes that differ greatly among themselves in the number of months or years that each covers. Additionally, the method works best with whole dentitions, while the Langebaanweg samples consist mainly of teeth that were isolated from jawbones during mining operations. These considerations leave crown height measurements as the most practical alternative for estimating the ages of individual Langebaanweg ungulates.

The mathematical relationship between advancing age and decreasing crown height has not been established for most living species and cannot be established for those from Langebaanweg, all of which are extinct. However, for hypsodont ungulates such as the Langebebaanweg species of concern here, it has been argued that the following assumptions permit useful estimates of age from crown height (Klein 1978; Klein *et al.* 1981):

- (i) that reduction in crown height is roughly constant through the life of a tooth, that is, that the relationship between decreasing crown height and advancing age is approximately linear;
- (ii) that for a deciduous tooth, the chronological age of complete crown reduction—when the crown is all but worn away—is the age when the tooth is replaced by a permanent tooth. For a permanent tooth, the chronological age of complete crown reduction is the age past which no individuals survive in the wild, sometimes known as 'potential ecological longevity'. The dental eruption/replacement schedules and potential ecological longevities of extinct species may be inferred from those of their closest living relatives of similar size and morphology. Estimates inferred for pertinent

Langebaanweg species are presented in Table 2. It is possible to show mathematically that only very large errors in these estimates will materially affect the shape of age profiles based on them (Klein *et al.* 1981);

(iii) that the amount of crown height lost per unit time on a deciduous tooth equals the initial unworn crown height divided by the time interval between age of eruption (usually birth) and age of replacement by a

TABLE 2

Ages of dental eruption and replacement and of potential ecological longevity inferred for the Langebaanweg species considered in this paper. All figures are in years.

	dP ⁴		P ⁴		Potential ecological longevity	Basis for inference
	Age of eruption	Age of replacement	Age of eruption	Age of replacement		
<i>Ceratotherium praecox</i>	0	6	6		35	Data on the dentally very similar black rhinoceros (<i>Diceros bicornis</i>) (Goddard 1970)
	dP ₄		M ₃		Age of replacement	Basis for inference
	Age of eruption	Age of replacement	Age of eruption	Age of replacement		
<i>Giraffa</i> sp.	0	4,5	3,5		28	Data on the dentally very similar modern giraffe (<i>Giraffa camelopardalis</i>) (Hall-Martin 1976)
<i>Sivatherium hendeyi</i>	0	6	4,67		37,24	Assumption that <i>S. hendeyi</i> parameters would exceed those of modern giraffe by roughly the same (1/3) proportion that <i>S. hendeyi</i> teeth exceed modern giraffe teeth in size
	dP ₄		M ₃		Potential ecological longevity	Basis for inference
	Age of eruption	Age of replacement	Age of eruption	Age of replacement		
<i>Mesembriportax acrae</i>	0	2,5	2		18	Data on extant bovids of similar size, such as Lichtenstein's hartebeest (<i>Alcelaphus lichtensteini</i>) (Mitchell 1965), black wildebeest (<i>Connochaetes gnou</i>) (Von Richter 1971, 1974), and greater kudu (<i>Tragelaphus strepsiceros</i>) (C. Simpson 1966)
<i>Simatherium demissum</i>	0	3,5	2,5		20	Assumption that <i>S. demissum</i> parameters would be smaller than those of the Cape buffalo (<i>Syncerus caffer</i>) (Grimsdell 1973; Sinclair 1977) by roughly the same (1/4) proportion that <i>S. demissum</i> teeth are smaller than Cape buffalo ones

permanent tooth. The amount of crown height lost per unit time on a permanent tooth equals the initial unworn crown height divided by the time interval between age of eruption and age at 'potential ecological longevity'. Initial crown height may usually be estimated from unworn or lightly worn teeth present in any sample large enough to calculate an age profile. The initial crown heights used in this study are presented in Table 3. It may be shown mathematically that only a very large error in estimated initial crown height will materially affect the shape of an age profile (Klein *et al.* 1981).

The key assumption here is that the rate of crown height reduction is constant. In the present context, it is pertinent that a more or less constant rate had been shown to characterize teeth of the Cape buffalo (*Syncerus caffer*)

TABLE 3

Initial unworn crown heights (in millimetres) used to calculate age profiles for Langebaanweg ungulate species considered in this paper. The initial unworn height of dP_4 in *Giraffa* sp. and of M_3 in both *Giraffa* sp. and *Sivatherium hendeyi* was taken as the mean height plus one standard deviation from the mean height of unworn specimens in the Langebaanweg samples. In the absence of any completely unworn specimens, the initial height of dP_4 in *S. hendeyi* was taken as the mean height plus one standard deviation from the mean height of thirteen very lightly worn specimens. *Giraffa* and *S. hendeyi* dP_4 's and M_3 's whose heights exceeded the calculated 'initial heights' were automatically assigned to the youngest age class possible.

The initial height of dP_4 in *Ceratotherium praecox* was estimated by adding 0,5 mm to the height of the highest tooth present, which was very lightly worn. The initial height of the *C. praecox* P^4 was taken as the height of the single unworn specimen present. In the absence of any unworn specimens, the initial height of dP_4 in *Mesembriportax acrae* was taken as 1 mm higher than the highest, lightly worn dP_4 in the Quartzose Sand Member sample. The initial height of the *M. acrae* M_3 was taken as 0,5 mm higher than the highest (very) lightly worn M_3 in the Bed 3aN sample. The initial height of the *Simatherium demissum* M_3 was estimated by adding 1,5 mm to the height of the highest-crowned M_3 present, which was lightly worn. There were no unworn or lightly worn *S. demissum* dP_4 's in the sample, so the initial crown height of this tooth was estimated by multiplying the ratio between *S. demissum* M_3 initial crown height and Cape buffalo M_3 initial height (36/53) by the initial height of the Cape buffalo dP_4 (24,0 mm), as determined in the author's previous work.

Given the variety of methods used to obtain initial crown heights, it is obvious that the values presented below are arbitrary to some extent, but it may be shown mathematically that only very large departures from these values would materially affect the shapes of the age profiles calculated from them.

	Initial (unworn) crown height (mm)	
	dP_4	P^4
<i>Ceratotherium praecox</i>	45,0	65,1
	dP_4	M_3
<i>Giraffa</i> sp.	16,3	27,8
<i>Sivatherium hendeyi</i>	23,4	45,1
<i>Mesembriportax acrae</i>	10,0	33,0
<i>Simatherium demissum</i>	16,3	36,0

(Grimsdell 1973) and of the giraffe (*Giraffa camelopardalis*) (Hall-Martin 1976), which are close living relatives of the Langebaanweg buffalo (*Simatherium demissum*) and giraffids (*Sivatherium hendeyi* and *Giraffa* sp.) respectively. A roughly constant rate has also been demonstrated in the Rocky Mountain elk (*Cervus canadensis*) (Klein *et al.* 1981), whose teeth are notably similar in size and morphology to those of Langebaanweg *Mesembriportax acrae*.

The elk study was undertaken specifically to check the reliability of the assumptions listed above. It was found that crown height was not a particularly accurate predictor of individual elk age, but the *distribution* of elk ages predicted from crown heights closely approximated the *distribution* of known ages, when both predicted and known ages were *grouped* into relatively broad, but analytically useful age classes. The age class used was based on 10 per cent of potential ecological longevity (approximately 16 years in elk, leading to a class interval of 1,6 years). 10 per cent of potential ecological longevity has also been used for grouping predicted ages within each species here, where it has the particular advantage of allowing direct comparison of age profiles among species that probably had very different potential longevity.

While the elk study strongly supported the use of crown heights to construct age profiles, it did suggest some modifications in the assumptions listed above. In particular, on average, elk shed their deciduous teeth before the crowns are completely worn away, and a better estimate of the (hypothetical) age of complete reduction in elk would be 'age of shedding plus 25 per cent'. On reflection, it seems likely that most ungulates shed their deciduous teeth before the crowns are completely reduced and 'age of shedding plus 25 per cent' has been used for each species in this study. Its principal effect is to place more individuals in the second 10 per cent of lifespan and fewer in the first. The elk study further suggested that permanent teeth which erupt later (e.g. M_2 or M_3) fit the assumptions of constant crown height reduction and of reduction to '0' at or very near 'potential ecological longevity' better than permanent teeth which erupt earlier (e.g. M_1). This result has been taken into account here as well.

In order to construct a profile that will include individuals of all possible ages within a species, crown heights must be measured on a category of deciduous teeth and on a category of permanent teeth. For *Langebaanweg Sivatherium hendeyi*, *Giraffa* sp., *Simatherium demissum*, and *Mesembriportax acrae*, dP_4 and M_3 were selected, mainly for the ease with which they may be recognized when isolated. In each species M_3 erupted before dP_4 was shed, so that the age profile produced from dP_4 crown heights overlaps with the one produced from the M_3 heights. In each case the overlap occurs in the second 10 per cent of lifespan, and the number of individuals assigned to that interval in the final (composite) age profile was based on either dP_4 or M_3 , whichever suggested the larger number.

In the rhinoceros, *Ceratotherium praecox*, dP_4 was shed before M_3 erupted. Use of these two teeth would thus automatically exclude some individuals, and it is obviously desirable to select another pair. Two further considerations affected the selection. First, it is difficult, if not impossible, consistently to distinguish M_1 from M_2 or M^1 from M^2 when these teeth are isolated, as most of the rhinoceros specimens were. Second, the structure of rhinoceros mandibular teeth suggests that their rate of wear may be exceptionally rapid just after eruption, seriously violating one of the assumptions behind the use of crown heights to predict age. The maxillary teeth appear structurally better suited to the assumptions. These considerations led to the selection of dP^4 and P^4 for construction of the rhinoceros age profile to be presented here, although, in fact, the one derived from dP_4 and P_4 is basically similar in shape and implications.

The dental dimension taken as crown height is essentially the same for all species and is illustrated in Figures 2 to 6. It is the minimum distance between the occlusal surface of a tooth and the base of the enamel, measured on the buccal face for mandibular teeth and on the lingual face for maxillary ones. On multilobed (or multilophed) teeth such as those of the species involved here, the measurement may be made on any lobe or loph. Measurements made on the anteriormost lobe (or loph) have been used to calculate the age profiles presented below, except in the case of *Sivatherium hendeyi*, where measure-

ments made on the second (or middle) lobe of M_3 were used. The reason is that many *S. hendeyi* M_3 's are broken, and the second lobe is easily identifiable as belonging to an M_3 , whereas the first is not. All measurements were made with Helios dial-reading calipers to the nearest tenth of a millimetre.

THE MORTALITY PROFILES AND THEIR IMPLICATIONS

Figures 2 to 6 present the age (mortality) profiles for each of the Langebaanweg species of concern here, as well as the crown height frequency distributions on which the profiles are based. The figures also show the frequency distributions of basal breadths for the same teeth whose crown heights were measured.

If each dental sample is truly homogeneous, basal breadths would probably be normally distributed, since normality is an almost universal characteristic of linear measurements on biological specimens. A significant departure from normality may indicate that dental size is sexually dimorphic or that a sample actually includes specimens from more than one species. (In either case, if enough specimens were included, the frequency distributions would be multimodal.) Applications of various tests suggested by Simpson *et al.* (1960) and Sokal & Rohlf (1969) to the Langebaanweg basal breadth distributions revealed only one significant departure from normality. This was for Bed 3aN *Mesembriportax acrae*, supporting the suggestion (above) that the sample may be taxonomically mixed.

Assuming that the relatively large samples available for *Sivatherium hendeyi*, *Giraffa* sp., and *Ceratotherium praecox* presumably reflect the populations from which they were drawn, the normal shape of the basal breadth distributions supports taxonomic homogeneity in each case and suggests that the dentitions of the species were not sexually dimorphic in size. (The alternative—that the teeth in each instance were drawn almost entirely from one sex—seems highly improbable). Perhaps even more important in the present context is that the heights of unworn crowns also appear to be distributed normally in those species (*Giraffa* sp. and especially *Sivatherium hendeyi*) where the samples of unworn crowns are reasonably large (Table 1). Generally speaking, marked sexual dimorphism in size is probably quite rare in ungulate dentitions (see, for example, the measurements on teeth of known sex in Klein 1974, 1975; Klein *et al.* 1981), which justifies ignoring sex in calculating age profiles from ungulate crown heights.

Examination of the mortality profiles presented separately in Figures 2 to 6 and recast as a group in Figure 7, shows that there are two basic types. In type one, characterizing *Sivatherium hendeyi* and *Giraffa* sp., individuals in the first 10 per cent of lifespan dominate heavily and successive lifespan segments include progressively fewer individuals, with very few beyond 40 per cent of potential lifespan. Type one is a classic 'catastrophic' mortality profile. In type two, characterizing *Ceratotherium praecox*, *Simatherium demissum*, and *Mesem-*

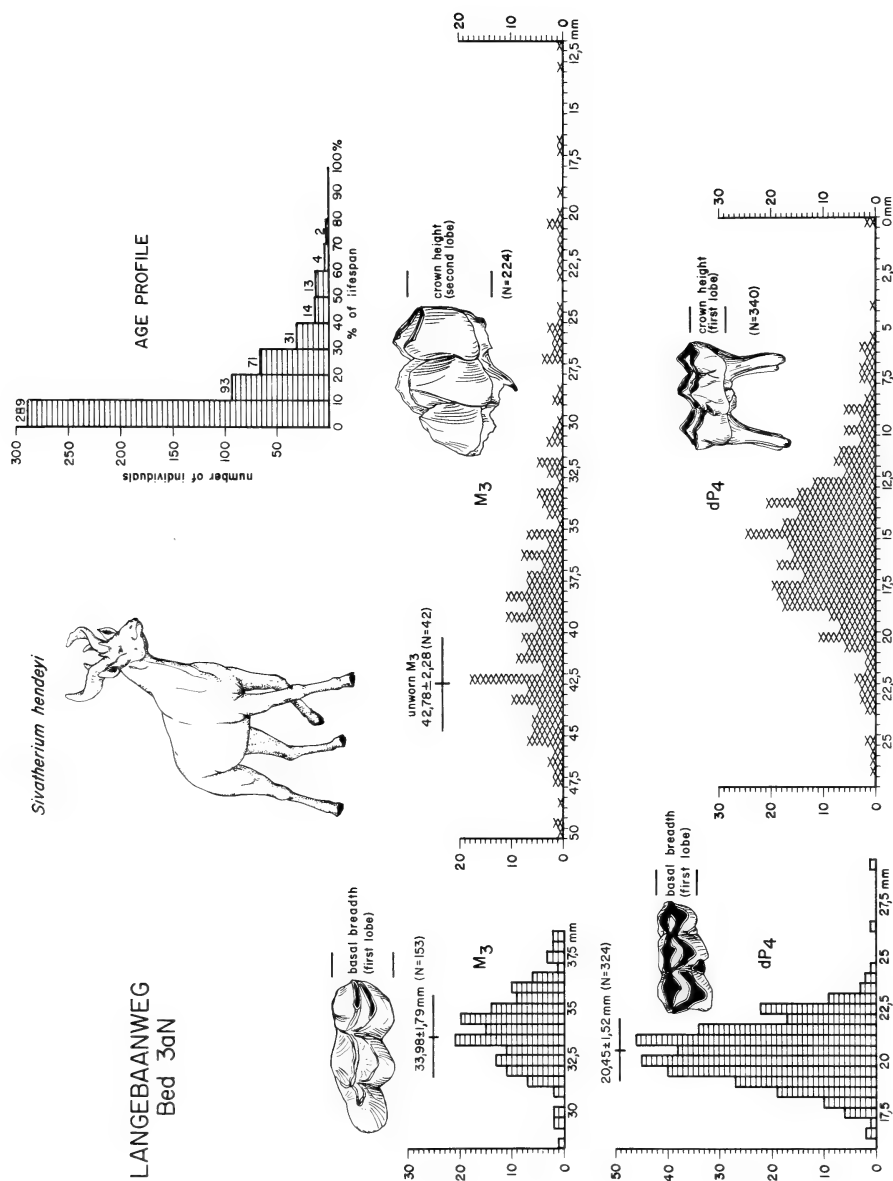


Fig. 2. The distribution of dP₄ and M₃ basal breadths and crown heights in the *Sivatherium hendeyi* sample from Bed 3aN of the Pelletal Phosphorite Member, Varswater Formation, Langebaanweg. The original measurements have been grouped into 0.5 mm classes. Means and standard deviations are presented for basal breadths and for the crown heights of unworn M₃'s. The age profile in the upper right-hand corner was calculated from the crown height distributions, as explained in the text.

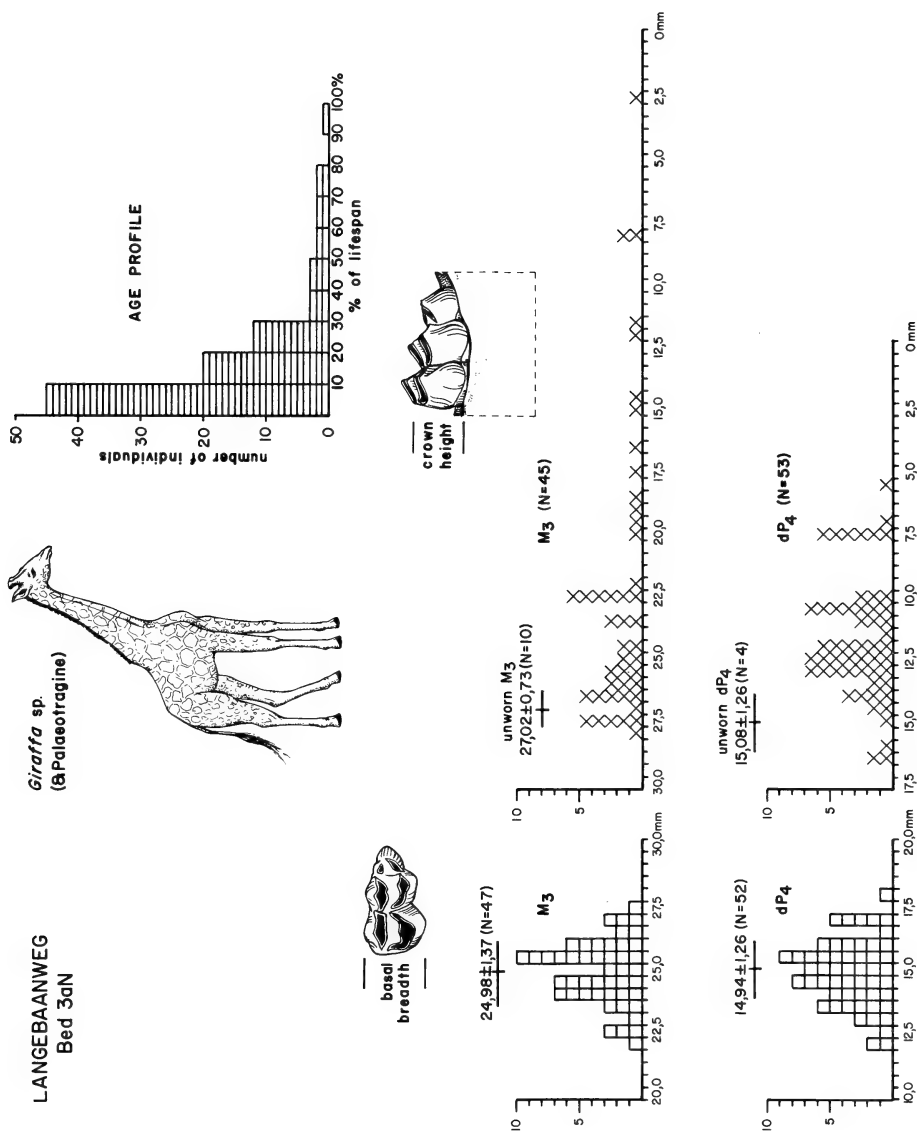


Fig. 3. The distribution of dP_4 and M_3 basal breadths and crown heights in the *Giraffa* sp. (and *Palaeotragine*) sample from Bed 3aN of the Pelletal Phosphorite Member, Varswater Formation, Langebaanweg. The original measurements have been grouped into 0,5 mm classes. Means and standard deviations are presented for basal breadths and for the crown heights of unworn teeth. The age profile in the upper right-hand corner was calculated from the crown height distributions, as explained in the text.

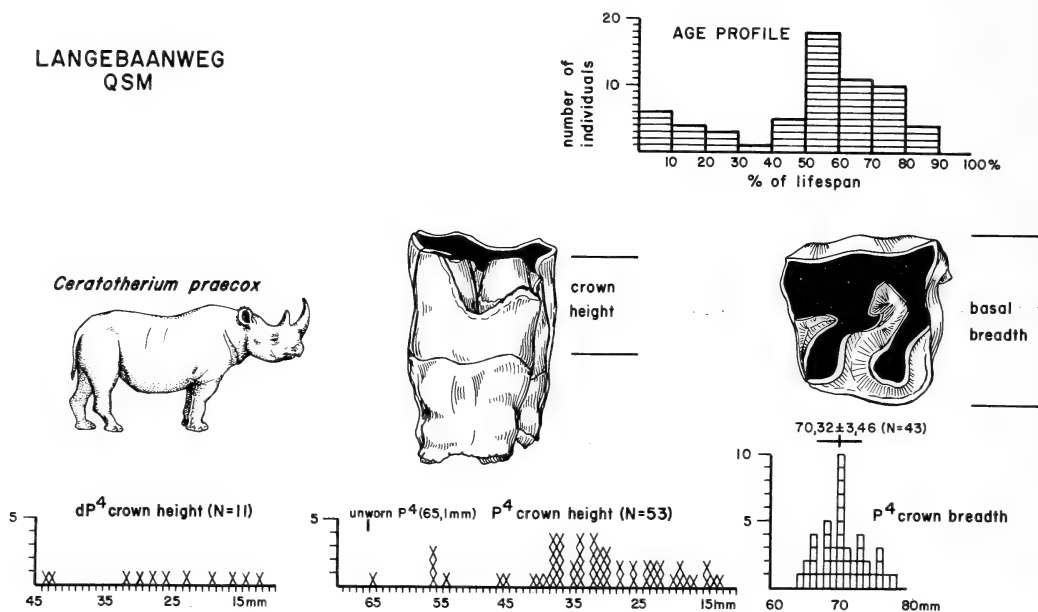


Fig. 4. The distribution of dP⁴ and P⁴ crown heights and of P⁴ crown breadths in the *Ceratotherium praecox* sample from the Quartzose Sand Member, Varswater Formation, Langebaanweg. The original measurements have been grouped into 1 mm classes. The mean and standard deviation are presented for P⁴ crown breadth. The age profile in the upper right-hand corner was calculated from the crown height distributions, as explained in the text.

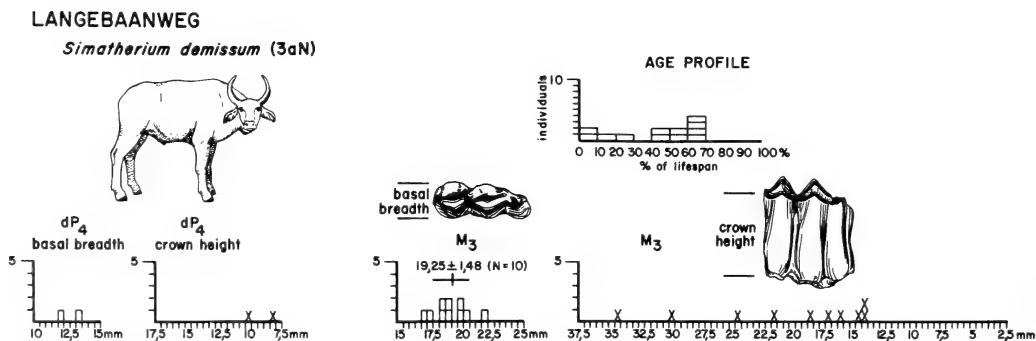


Fig. 5. The distribution of dP₄ and M₃ basal breadths and crown heights in the *Simatherium demissum* sample from Bed 3aN of the Pelletal Phosphorite Member, Langebaanweg. The original measurements have been grouped into 0,5 mm classes. The mean and standard deviation of M₃ breadth are presented. The age profile in the upper right-hand corner was calculated from the crown height distributions, as explained in the text.

Mesembriportax acrae

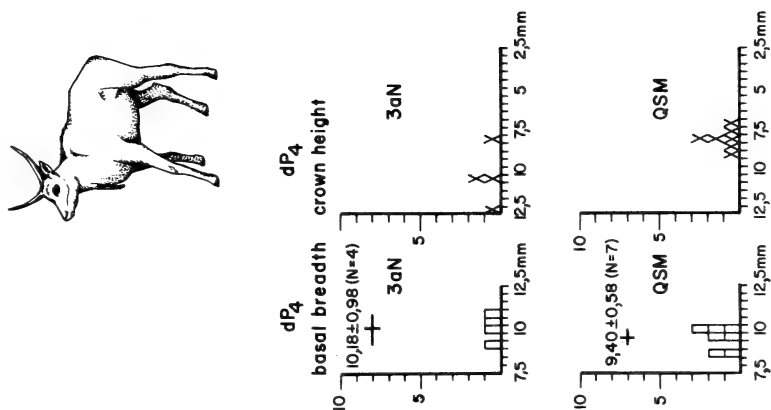


Fig. 6. The distribution of dP_3 and M_3 basal breadths and crown heights in the *Mesembriportax acrae* samples from the Quartzose Sand Member and from Bed 3aN of the Pelletal Phosphorite Member, Varswater Formation, Langebaanweg. The original measurements have been grouped into 0.5 mm classes. Means and standard deviations are presented for basal breadths. The age profiles in the upper right-hand corner were calculated from the crown height distributions, as explained in the text.

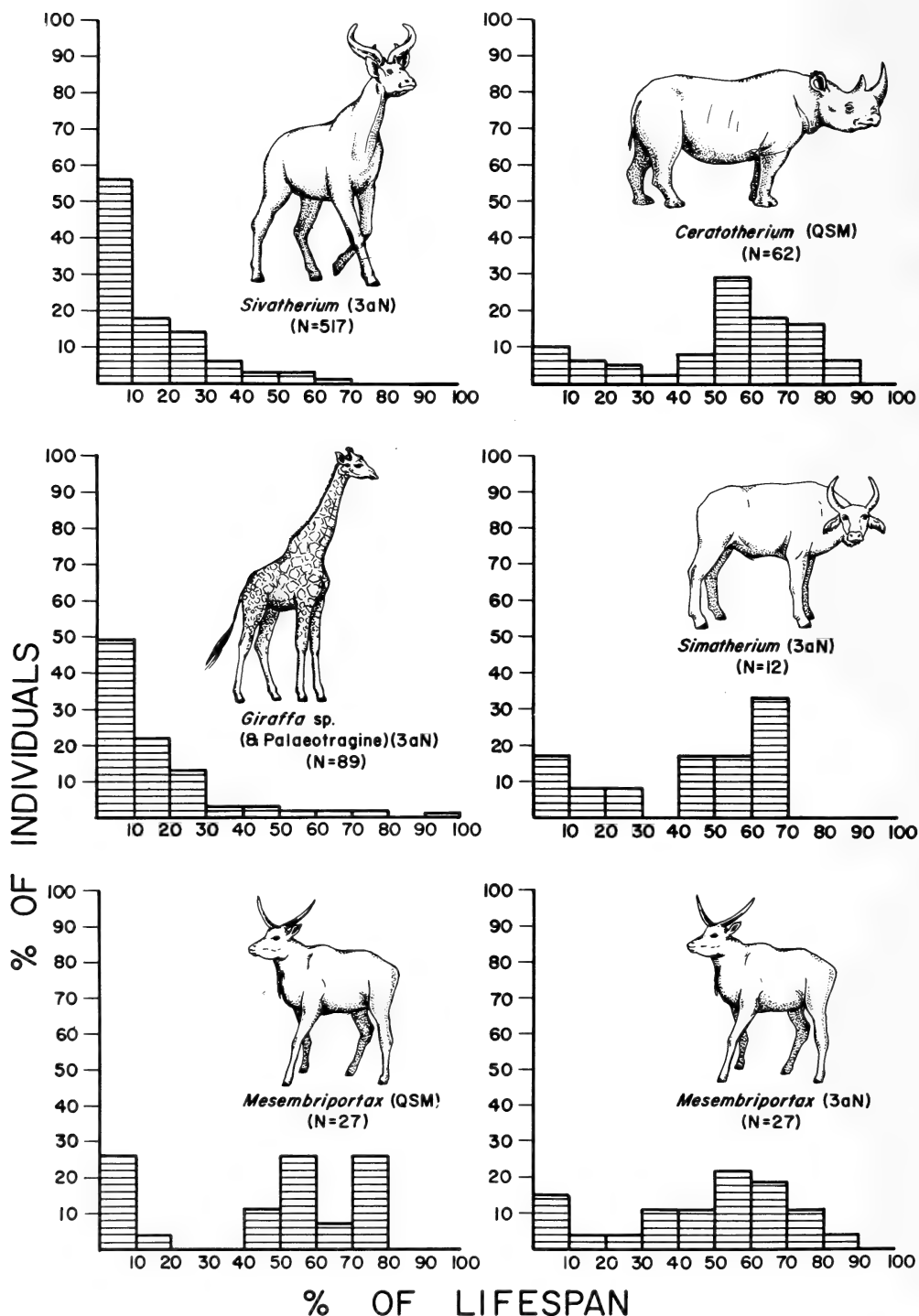


Figure 7.

briportax acrae, individuals beyond 40 per cent of lifespan predominate heavily and ones in lifespan segments between 10 and 40 per cent are particularly infrequent. Type two would be a classic 'attritional' mortality profile, except for the relative rarity of individuals in the first 10 per cent of lifespan. Application of the Kolmogorov–Smirnov test (results in the caption of Fig. 7) supports the assertion that the *Sivatherium* and *Giraffa* profiles resemble each other and differ from those of the other species, which are, however, similar to each other.

The catastrophic shape of the *Sivatherium* and *Giraffa* mortality profiles clearly suggests that the individuals present in the Bed 3aN channel fill were victims of drowning, and thus that their superabundance versus other species in the deposit may reflect a greater tendency to remain near the river during flood periods. The most likely explanation for this behaviour is that the trees on which the giraffids browsed were largely restricted to the immediate vicinity of the river. Other species, such as the rhinoceros and the boselaphine, which probably browsed on understorey plants, and the buffalo and alcelaphines, which were probably grazers, were probably attracted away from the river during flood intervals by the vegetation flush and more widely available surface-water accompanying rains.

After the giraffids, the alcelaphines are the most common species in Bed 3aN, and it is possible that, their food preferences aside, they were more prone than other species to attempt to cross the river in flood periods. Together with a reduction in the density of woodland along the river, this could account for the superabundance of alcelaphines v. other species in Bed 3aS. Although the alcelaphine crown heights have yet to be measured, subjective examination suggests that they will provide 'catastrophic' age profiles at least broadly similar to the giraffid ones.

Assuming that the giraffids are the most common species in the Bed 3aN channel fill because they were more likely than other species to be caught in floods, it would obviously be interesting to know whether flooding was seasonal

Fig. 7. Age profiles of *Sivatherium hendeyi*, *Giraffa* sp. (and Palaeotragine), *Ceratotherium praecox*, *Simatherium demissum*, and *Mesembriportax acrae* in the Quartzose Sand Member and in Bed 3aN of the Pelletal Phosphorite Member, Varswater Formation, Langebaanweg. The Kolmogorov–Smirnov results below indicate that the profiles of *S. hendeyi* and *Giraffa* sp. are statistically indistinguishable from one another, but differ significantly from the profiles of other species, which are in turn statistically indistinguishable from one another. A Kolmogorov–Smirnov value of 1,36 implies a difference significant at the 0,05 level; a value of 1,63 implies a difference significant at the 0,01 level. Values reflecting a difference significant at the 0,05 level or below are underlined.

	<i>Siva- therium hendeyi</i> (3aN)	<i>Cerato- therium praecox</i> (QSM)	<i>Giraffa</i> sp. (and Palaeo- tragine) (3aN)	<i>Mesembri- portax acrae</i> (QSM)	<i>Sima- therium demissum</i> (3aN)
<i>Sivatherium hendeyi</i> (3aN)	—				
<i>Ceratotherium praecox</i> (QSM)	<u>4,99</u>	—			
<i>Giraffa</i> sp. (and Palaeotragine) (3aN)	<u>0,70</u>	<u>3,87</u>	—		
<i>Mesembriportax acrae</i> (QSM)	<u>3,24</u>	<u>0,69</u>	<u>2,59</u>	—	
(3aN)	<u>3,29</u>	0,61	<u>2,78</u>	0,44	—
<i>Simatherium demissum</i> (3aN)	<u>2,09</u>	0,59	<u>1,76</u>	0,75	0,40

or not. If the giraffids were seasonally restricted breeders, as most modern African ungulates are (Mentis 1972), and if flooding were seasonal, crown height distributions such as those in Figures 2 and 3 could be expected to exhibit patterned multimodality (Kurtén 1953). Successive modes representing cohorts of individuals with average birth dates a year apart would be separated by equidistant gaps representing the average amount of crown height lost by each cohort between flood seasons.

Clearly, neither the *Sivatherium* nor the *Giraffa* crown height distributions in Figures 2 and 3 exhibit the kind of multimodality from which seasonality may be reasonably inferred. In the case of the *Giraffa* distributions, the reason may be relatively small sample size. In the case of the *Sivatherium* distributions, based on much larger samples, the reason may be that the species bred more or less throughout the year or that flooding (drowning) was not seasonal. In modern *Giraffa camelopardalis*, the closest living relative of *Sivatherium*, breeding peaks tend to be subtle or absent (Mentis 1972; Foster & Dagg 1972). However, it is also important to point out that *Sivatherium hendeyi* was relatively low-crowned, particularly relative to (inferred) potential individual lifespan. This means that even if breeding were seasonal, the average amount of crown height lost by an age cohort each year was relatively small and there was probably substantial overlap in crown heights between individuals of adjacent cohorts. The detection of patterned multimodality reflecting seasonal births and deaths may therefore require truly enormous samples. It is pertinent here that the author failed to find multimodality in a large sample of similarly low-crowned elk, in which seasonally restricted births and deaths were historically documented (Klein *et al.* 1981). Overall then, the giraffids are probably less than ideal species for testing the hypothesis of seasonal bone accumulation at Langebaanweg. Far more appropriate would be the alcelaphines, because they are far more hypsodont relative to (inferred) potential lifespan and because their close living relatives often exhibit well-defined birth peaks. Additionally, alcelaphine teeth are superabundant in the Bed 3aS channel fill. The possibility of using them to detect seasonal mortality is added reason for measuring their crown heights in the near future.

The mortality profiles of *Ceratotherium praecox* and *Mesembriportax acrae* in the QSM only partly support the *a priori* suggestion that QSM species would exhibit attritional patterns. This is because individuals in the first 10 per cent of lifespan are seriously underrepresented relative to their probable level of mortality from attritional factors. The situation is similar to that noted by Sinclair (1977) for Cape buffalo on the Serengeti Plain and by Goddard (1970) for black rhinoceros in Tsavo National Park. In both instances, large samples of skulls observed in the field included remarkably few individuals in the first 10 per cent of lifespan, though such individuals were known to be characterized by relatively high mortality, as in free-ranging large mammal populations generally. In both instances, the rarity of young skulls is attributed to their greater tendency to disintegrate from weathering or to be broken up by carnivores.

Assuming that the relative lack of very young individuals in the QSM profiles at least partly reflects carnivore destruction or removal of bones before burial, it becomes especially interesting that very young individuals are extremely well represented in 'attritional' profiles constructed from the crown heights of large ungulates in late Pleistocene archeological and carnivore (probable *Hyaena brunnea*) bone accumulations in southern Africa (Klein 1978 and unpublished). With regard to the archeological sites, the implication would be either that the occupants were expert at locating the carcasses of very young animals before carnivores destroyed them or removed parts to dens, or that the occupants themselves were active predators on very young animals. The latter alternative seems more plausible, given the likely desire of hominids to avoid conflict with other potential scavengers whose special senses would probably bring them to a carcass first. These considerations lead to the further suggestion that early Pleistocene hominids, hypothetically relying more heavily on scavenging, would probably produce a bone accumulation in which 'attritional' profiles were relatively deficient in very young individuals, similar to those from Langebaanweg, rather than those from later Pleistocene archeological sites.

The age profiles of Bed 3aN *Simatherium demissum* and *Mesmbriportax acrae* require comment not because they are relatively deficient in very young individuals, but because they are clearly not 'catastrophic' in a deposit where it has already been shown that catastrophic death took place. In the case of Bed 3aN *M. acrae*, it is possible that the profile has been distorted from catastrophic shape by taxonomic admixture in the sample (see above), though it is difficult to see how admixture could have this effect. Overall, since both the *S. demissum* and *M. acrae* profiles in Bed 3aN closely resemble those of the QSM species, it seems most likely that they are based on dentitions which were either reworked from the QSM deposits or which were washed off the floodplain adjacent to the 3aN channel. One obvious test of this hypothesis would be to examine bones of Bed 3aN *S. demissum* and *M. acrae* to see if they exhibit patterns of weathering or carnivore-gnawing different from those of the 3aN giraffids and perhaps similar to those of the QSM species. This will be an aspect of future research.

SUMMARY AND CONCLUSIONS

The mortality profiles constructed from dental crown heights of five Langebaanweg ungulate species belong to two clearly distinct types. Type one, in which individuals in the first 10 per cent of potential lifespan predominate and in which there are progressively fewer individuals in each succeeding lifespan segment, characterizes the giraffids, *Sivatherium hendeyi* and *Giraffa* sp., found in the channel fill deposits of Bed 3aN. The shape of the profile suggests that the giraffids died catastrophically, probably by drowning during periods of high river flow. This suggests in turn that the giraffids are superabundant v. other species in the channel fill because they were more inclined to remain near the river during flood periods. The most plausible explanation of this behaviour is that the trees on which they browsed were largely confined to the river margins.

Other species with different feeding-habits were probably attracted away from the river during flood intervals by a rain-induced vegetation flush and increase in surface water.

In the second type of mortality profile, characterizing the rhinoceros *Ceratotherium praecox* and the boselaphine antelope *Mesembriportax acrae* in the floodplain sediments of the Quartzose Sand Member, and the buffalo *Simatherium demissum* and the boselaphine *M. acrae* in Bed 3aN, individuals beyond 40 per cent potential lifespan predominate and there are relatively few individuals in lifespan segments between 10 and 40 per cent. The shape of the profiles suggests death by natural attrition (from predation, endemic disease, etc.), though individuals in the first 10 per cent of lifespan are under-represented v. their probable level of natural mortality. This is probably because their bones were particularly susceptible to weathering or to destruction or removal by carnivores before burial. The fact that the Bed 3aN profiles of *S. demissum* and *M. acrae* are very similar to those of QSM *acrae* suggests that the bones of *S. demissum* and *M. acrae* in the 3aN channel fill were either reworked from older (QSM) deposits or swept off the floodplain adjacent to the 3aN channel.

Assuming that the under-representation of very young individuals in the Langebaanweg 'attritional' profiles at least in part reflects differential carnivore destruction or removal of their bones v. those of older animals, it is potentially meaningful that very young individuals are very well represented in 'attritional' age profiles of large ungulates in late Pleistocene archeological sites in southern Africa. Since the late Pleistocene people were probably much less successful at locating fresh carcasses than other predators and/or scavengers, the implication is that they actively preyed on the young animals. If, as logic suggests, earlier Pleistocene hominids were more dependent on scavenging (and less successful at hunting), it follows that attritional profiles of ungulates in their sites would resemble the Langebaanweg ones in the under-representation of very young individuals.

The Langebaanweg assemblage includes several other species which are sufficiently well represented to permit construction of mortality profiles. Most promising in terms of their abundance are the alcelaphines, *Damalacra neanica* and *D. acalla*, which probably also have the greatest potential for revealing whether flooding by the ancient Langebaanweg River was seasonal or not. In future research with the Langebaanweg assemblage, the author will focus on measurement and analysis of the alcelaphine material, as well as on age (and possible sex) determination in other well-represented species.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

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R. G. KLEIN

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(continued inside back cover)

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THE SYNONYMIZATION OF *TRIODOS*
K. H. BARNARD WITH *AMPELISCA* KRÖYER
(CRUSTACEA, AMPHIPODA)

By

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&

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Cape Town Kaapstad

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THE SYNONYMIZATION OF *TRIODOS* K. H. BARNARD WITH *AMPELISCA* KRÖYER (CRUSTACEA, AMPHIPODA)

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(With 3 figures)

[MS accepted 8 April 1981]

ABSTRACT

The genus *Triodos* K. H. Barnard 1916, is re-examined and synonymized with the genus *Ampelisca* Kröyer, 1842 (family Ampeliscidae). The type species, *Triodos insignis* K. H. Barnard, 1916, is redescribed and figured and removed to *Ampelisca* as a valid species. The validity of the genus *Byblis* is discussed.

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INTRODUCTION

During our work on the revision of the families and genera of the World Gammaridea (monograph in preparation), the validity of two genera in the family Ampeliscidae was studied.

We re-examined the type species of the genus *Triodos*, *T. insignis* K. H. Barnard, 1916, described from South Africa, because the original description was poorly illustrated and the exact taxonomic position of the genus was uncertain.

Based on our study, *Triodos insignis* is removed to the genus *Ampelisca* Kröyer as a valid species, and the genus *Triodos* K. H. Barnard, 1916, is synonymized with *Ampelisca* Kröyer.

Ampelisca Kröyer, **new synonymy**

Ampelisca Kröyer, 1842: 154 (*Ampelisca eschrichtii* Kröyer, 1842, monotypy). Stebbing, 1906: 98. J. L. Barnard, 1960: 3 (including key to species). G. S. Karaman, 1975: 5.
Pseudoptalmus [sic] Stimpson, 1853: 57 (*Pseudoptalmus pelagicus* Stimpson, 1853, here selected, = *Ampelisca eschrichtii* Kröyer, 1842).
Araneops Costa, 1853: 169 (*Araneops diadema* Costa, 1853, here selected).
Tetromatus Bate, 1857: 139 (*Tetromatus typicus* Bate, 1857, here selected).
Triodos K. H. Barnard, 1916: 140 (*Triodos insignis* K. H. Barnard, 1916, original designation) [new synonym].

INVALIDITY OF *TRIODOS*

K. H. Barnard (1916) described *Triodos insignis* a new genus and species from South Africa (off the Umhloti River, depth 100 fathoms).

At p. 140 he wrote that this genus 'combines in a remarkable manner the characters of the three hitherto recognized genera of Ampeliscidae'. Because this species was very poorly figured, later workers considered the head to have a produced anteroventral corner and pereopod 7 to be like that in *Ampelisca*.

After detailed examination of *Triodos insignis* from new material, it was evident that it belongs to the genus *Ampelisca* with a short head such as that of other species (*A. rubella* Costa, 1864, etc.). All other taxonomic characters of *T. insignis* are identical with those of members in the genus *Ampelisca*.

The distoposterior lobe of article 2 on pereopod 7 has at the anteroventral margin of the lobe one seta more than is usual in the genus *Ampelisca*, but *Ampelisca rubella*, and *Ampelisca spinimana* Chevreux, 1887a also have one to two setae at the anteroventral corner on the distoposterior lobe of article 2 on pereopod 7. For this reason, the pilosity of pereopod 7 in *T. insignis* belongs to the *Ampelisca* form.

Ampelisca insignis (K. H. Barnard), **new combination**

Figs 1–3

Triodos insignis K. H. Barnard, 1916: 140, pl. 26 (figs 8–10). J. L. Barnard, 1969: 132. Griffiths, 1974: 223; 1975: 104.

*Description**Female*

8.6 mm with nonsetose oostegites. Body smooth except last metasomite and urosomites; last metasomite with two dorsoposterior plumose setae (Fig. 3A); urosomites 1–2 elevated, triangular in lateral view (Fig. 3E), laterally compressed, bearing one row of short plumose setae along each lateral side; urosomites 2–3 coalesced.

Coxae 1–4 longer than broad, with convex distal (= ventral) margin provided with one row of long plumose setae, without distinct marginal notch. Coxa 1 dilated distally (Fig. 2A), coxa 4 with well-developed distoposterior lobe produced sharply in proximal part (so that lateral margins of coxa 4 are not parallel (Fig. 2D)).

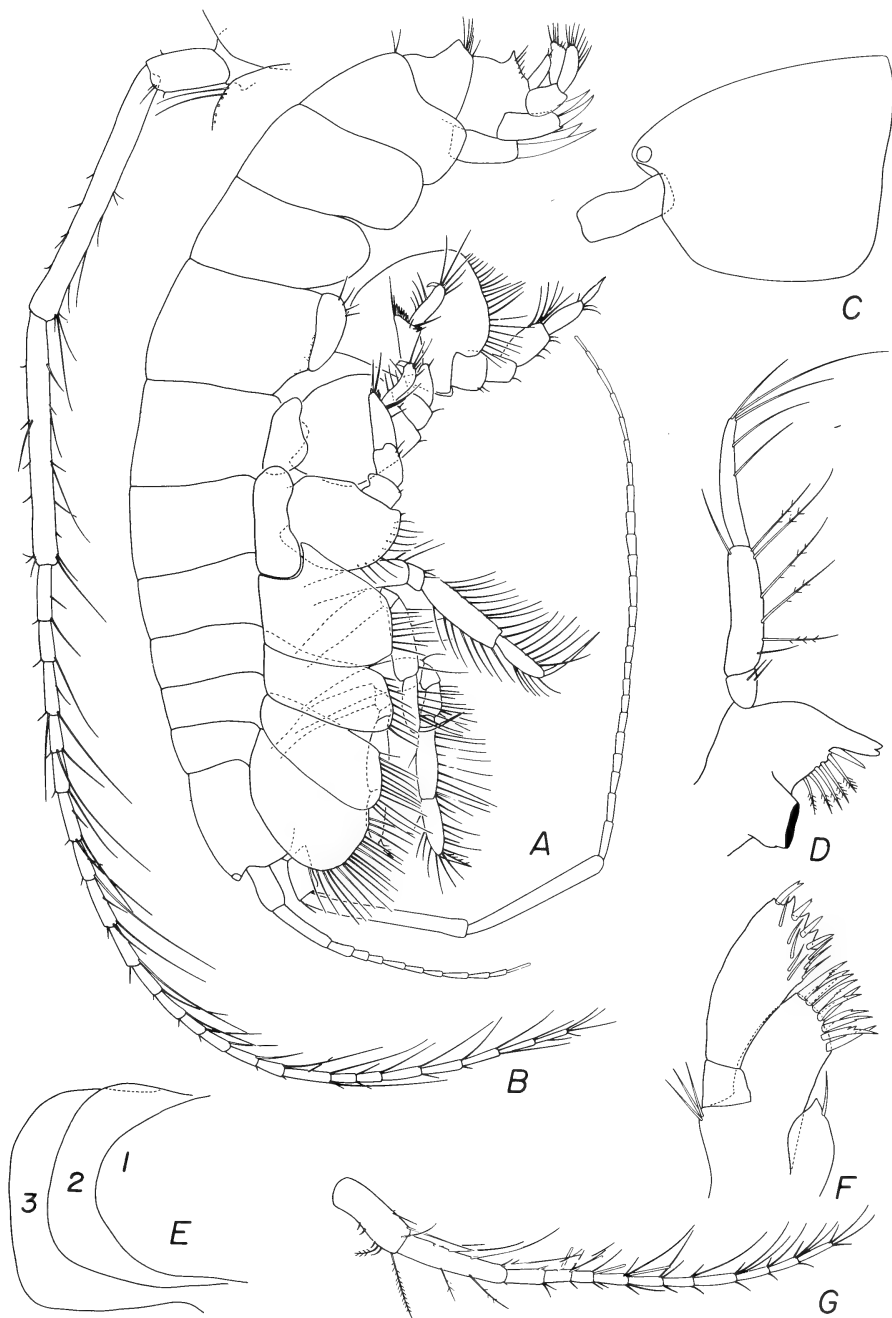


Fig. 1. *Ampelisca insignis* (K. H. Barnard), female 8,6 mm. A. Lateral body. B. Antenna 2. C. Lateral head. D. Left Mandible. E. Epimera 1-3, number placed near posteroventral corner of each. F. Maxilla 1 (11th spine on outer plate hidden). G. Antenna 1.

Epimeral plates 1–3 smooth, nearly subrounded (Fig. 1E).

Head longer than first two pereonites combined, obtuse (Fig. 1C), scarcely longer than tall, with short rostrum; lateral cephalic lobes obtuse, straight, anteroventral corner not produced nor pointed, like those in many other *Ampelisca* species (*A. rubella*, etc.). One corneal lens present on each side near dorsoanterior tip of head.

Antenna 1 short, slender, slightly exceeding peduncular article 4 of antenna 2 (Fig. 1A); peduncular article 2 of antenna 1 slightly longer than article 1, article 3 short; accessory flagellum absent; main flagellum longer than peduncle, consisting of 9 articles, some of them with one aesthetasc each (Fig. 1G).

Antenna 2 long, nearly as long as body: peduncular article 3 short, peduncular article 4 scarcely longer than 5, slender (Fig. 1B); flagellum 23-articulate, bearing long setae.

Labrum incised distally (Fig. 2F), broader than long (tall). Labium normal, with well-developed inner lobes (Fig. 2B).

Mandible with well-developed strong triturative molar, incisor toothed; palp 3-articulate, article 1 short, articles 2–3 subequal in length, setose, non-falciform, not dilated distally (Fig. 1D).

Maxilla 1: inner lobe with 1 simple seta, outer lobe with 11 spines (Fig. 1F showing only ten), provided with one to four lateral teeth each; palp 2-articulate, second article dilated distally, provided with distal teeth accompanied by several spines and subdistal setae.

Maxilla 2 with narrowed lobes, inner lobe without dorsal oblique row of setae (Fig. 2E).

Maxilliped: inner lobe short, with two distal spines intermixed with several plumose setae; outer lobe reaching tip of second palp article, bearing one row of strong spines along inferior margin; palp 4-articulate, palp article 3 not lobed, article 4 with nail shorter than remaining part of article (Fig. 2C).

Gnathopods 1–2 linear, simple, gnathopod 1 shorter than gnathopod 2 (Fig. 2A, I). Gnathopod 1: article 5 longer than 6, densely setose along margins; article 6 tapering distally, with dactyl shorter than article 6, bearing 4 setae along inferior margin and 1 seta at outer margin.

Gnathopod 2: article 5 linear, long, densely setose; article 6 much shorter than 5, tapering distally, dactyl with five setae along inferior margin and with one seta at outer margin (Fig. 2I).

Pereopod 3 linear, with articles 4–6 bearing long plumose setae along both margins; article 4 slightly inflated; dactyl slender, straight, longer than article 6 (Fig. 3B).

Pereopod 4 like that of pereopod 3, but slightly longer (Fig. 2D). Pereopod 5: article 2 ovoid, with short distoposterior lobe and with smooth posterior margin, anterior margin with one row of plumose setae; articles 3–4 short (Fig. 2G); article 5 produced distoposteriorly, bearing one row of short spines on apex; article 6 with long distal setae, dactyl short, nail-shaped, with two dorsal teeth.

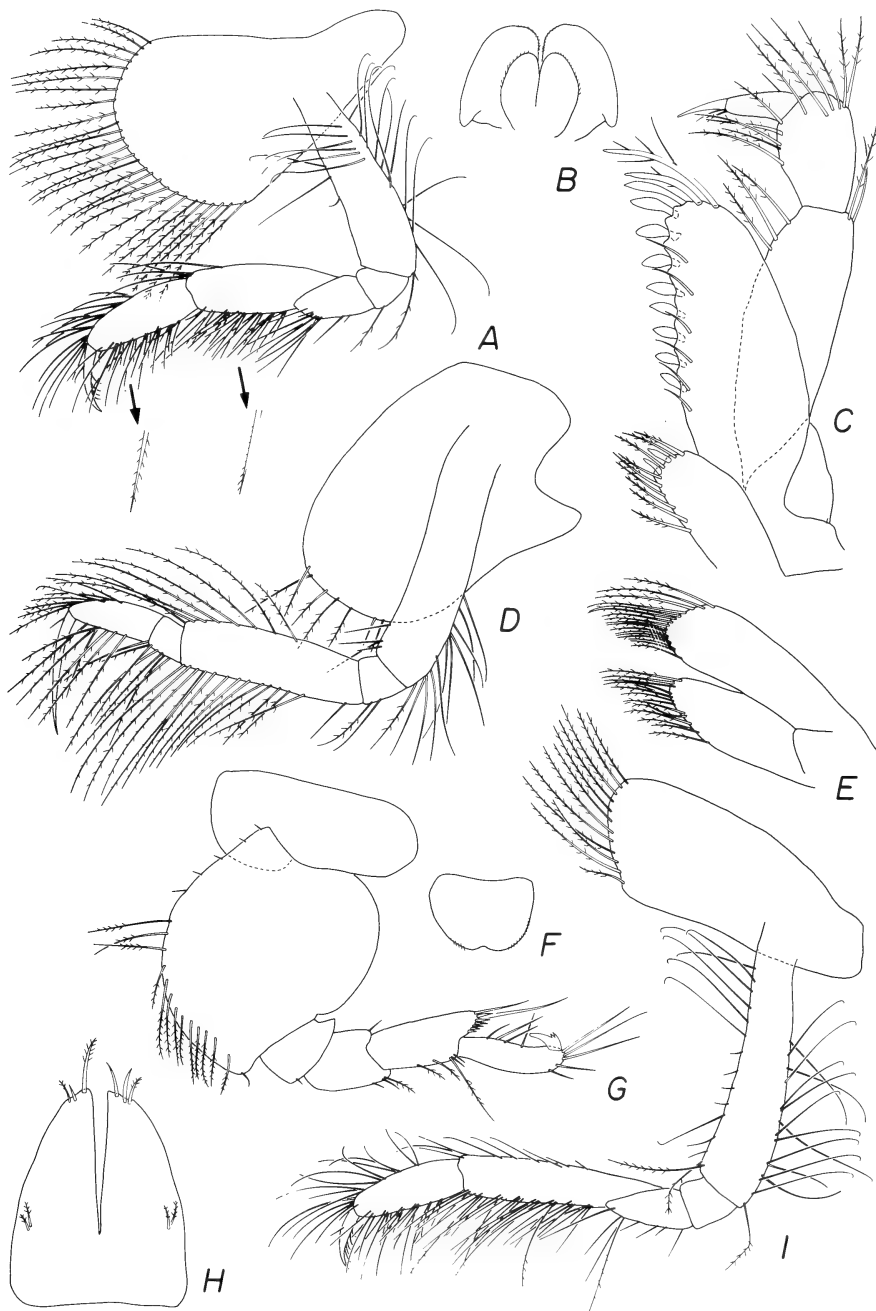


Fig. 2. *Ampelisca insignis* (K. H. Barnard), female 8,6 mm. A. Gnathopod 1. B. Lower lip. C. Maxilliped. D. Pereopod 4. E. Maxilla 2. F. Upper lip. G. Pereopod 5. H. Telson. I. Gnathopod 2. D and G = medial view.

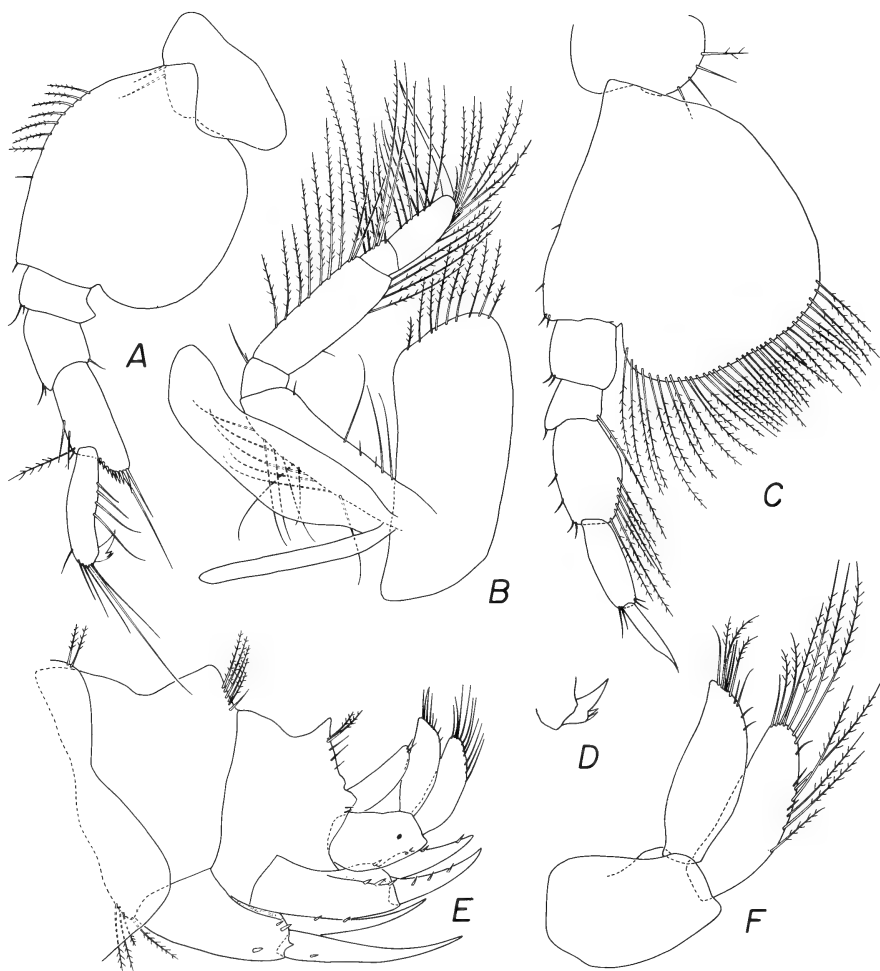


Fig. 3. *Ampelisca insignis* (K. H. Barnard), female 8,6 mm. A. Pereopod 6. B. Pereopod 3. C. Pereopod 7. D. Dactyl of pereopod 6. E. Lateral urosome (inner ramus of uropod 1 pulled laterally to show spines). F. Uropod 3. A, B and C = medial view.

Pereopod 6: article 2 with stronger distoposterior lobe and less setose anterior margin than those of pereopod 5; articles 3–7 like those of pereopod 5 (Fig. 3A).

Pereopod 7: nearly as long as pereopod 6, but of different shape: article 2 very large, dilated medially, with large distoposterior lobe reaching distal tip of article 3 (Fig. 3C), bearing numerous plumose setae along posterior and ventral margins; article 3 short; article 4 shorter than 3, poorly produced at distoanterior tip and bearing one long distoposterior seta; article 5 slightly inflated, longer than broad, bearing one row of plumose setae along distoposterior margin;

article 6 slightly shorter and narrower than 5, almost smooth; dactyl narrow, almost as long as article 6, spiniform.

Pleopods well developed, normal, with two retinacula each.

Uropods 1–2 short. Uropod 1: peduncle stout, poorly spinose (Fig. 3E), rami slender, pointed distally, almost smooth, outer ramus slightly longer than inner. Uropod 1 only slightly exceeding apex of peduncle of uropod 2.

Uropod 2: peduncle stout, longer than rami, poorly spinose (Fig. 3E), rami nearly subequal, stouter than these on uropod 1, bearing spines along margins.

Uropod 3 short, but strongly exceeding apex of uropod 2: peduncle stout, scarcely shorter than ramus (Fig. 3F), smooth; rami almost subequal, bearing plumose setae along outer margin, uniarticulate, almost foliaceous, inner ramus tapering distally.

Telson much exceeding apex of peduncle on uropod 3, longer than broad, incised two-thirds of its length (Fig. 2H); each lobe tapering distally, bearing several setae, one pair of short sensory setae occurring on proximal part of each lobe.

Male

Unknown.

Variability

Epimeral plates 1–3 more or less subrounded.

Material examined

South Africa: WCD 229 Z, University of Cape Town, Ecological Survey, 4 specimens (figured female 8.6 mm).

Localities cited

South Africa: Umhloti River mouth NW 1/2 W., distant 15 miles (Natal), 100 fathoms (K. H. Barnard 1916, Griffiths 1974); summary below indicated by Griffiths (1975).

Distribution

Cape of Good Hope to Natal, South Africa, 183 m.

Remarks

Ampelisca misakiensis Dahl (1944) (and see Imbach 1969; Nagata 1965; Margulis 1968) is so close to *A. insignis* that it may, at best, represent only a subspecies. Imbach showed considerable variability in the head of *misakiensis* in the South China Sea, whereas Dahl described a head quite close to that of *insignis* in his Japanese material. If all the specimens identified by Imbach are indeed a single species, then a great deal of variability does exist and we therefore cannot find any distinctions between *insignis* and *misakiensis*. They have many characters in common which are rather unusual in *Ampelisca*: both

urosomite 1 and urosomites 2–3 (fused) have a dorsal process (not in all Imbach specimens and poorly in Dahl figure), lateral facial spine(s) on peduncle of uropod 1, and setal creep on article 2 of pereopod 7 (setae creeping on to anterior margin of main lobe). The Japanese specimens and some specimens of the South China Sea from Imbach have the large rostrum on which the ocular lenses are found, but Imbach also shows specimens with the small rostral area as in *insignis*.

Before *misakiensis* is made a synonym of *insignis*, the South China Sea specimens of Imbach should once again be examined and work should be done on the occurrence of the species all through the Indian Ocean, from Indo-China to South Africa.

THE PROBLEM OF THE GENUS *BYBLIS*

Byblis Boeck, 1871, is very similar to *Ampelisca* but differs from the latter (*sensu auctorum*) by (i) article 2 of pereopod 7 being provided with setae at the ventroanterior margin near its conjunction with article 3; (ii) short, obtuse telson, incised up to half of its length; and (iii) the narrow article 7 of pereopod 7. These are further discussed below.

(i) The condition of pilosity on article 2 of pereopod 7 cannot be accepted as a distinctly valid character for separating the genera *Byblis* and *Ampelisca* from each other because of the observed transition in shape of this character among many species of both genera. For example, article 2 of pereopod 7 lacks any setae at the ventroanterior margin near its conjunction with article 3 (*Ampelisca sarsi* Chevreux, 1887b, *A. brevicornis* Costa, 1853, and many other species of *Ampelisca*); article 2 of pereopod 7 has one or two setae at the anteroventral margin near its conjunction with article 3 (*A. insignis*, *A. cucullata* J. L. Barnard, 1954, *A. misakiensis* Dahl, 1944, *A. iyoensis* Nagata, 1959; article 2 of pereopod 7 has numerous setae at the anteroventral margin near its conjunction with article 3, like species in the genus *Byblis* (for example *B. cyclops* Walker 1904, see Imbach 1969, pl. 5)

(ii) The shape of the telson seems to be the only good character at the moment separating the genera *Ampelisca* and *Byblis*. The telson in *Byblis* is as long as broad or broader than long, obtuse distally, incised maximally up to half of the telsonic length—although *Ampelisca agassizi* (Judd, 1896) (= *compressa* Homes, 1905, = *vera* J. L. Barnard, 1954, see Mills, 1967) also bears an obtuse telson; *Byblis serrata* Smith, 1873, also has a telson tapering distally like *Ampelisca*, but it is incised only half-way. On the other hand, *Ampelisca cyclops* Walker, 1904, has a telson like normal *Ampelisca* but incised scarcely more than half of its length.

(iii) The shape of article 7 (dactyl) of pereopod 7 is a problematic taxonomic character because of its large variability within the species and populations of *Ampelisca* (see *A. iyoensis* in Imbach, 1969).

For the moment, we retain *Ampelisca* and *Byblis* as distinct because of the different shapes of the telson, but the discovery of new species may require synonymization of the genera.

ACKNOWLEDGEMENTS

We thank Dr C. L. Griffiths of the Zoology Department, University of Cape Town, for lending us material of *Triodos insignis* and Dr T. H. Barry, Director of the South African Museum, for his kind assistance in this matter. We also thank Irene F. Jewett who inked our drawings for press, Elizabeth B. Harrison and Janice Clark who helped us prepare the text.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

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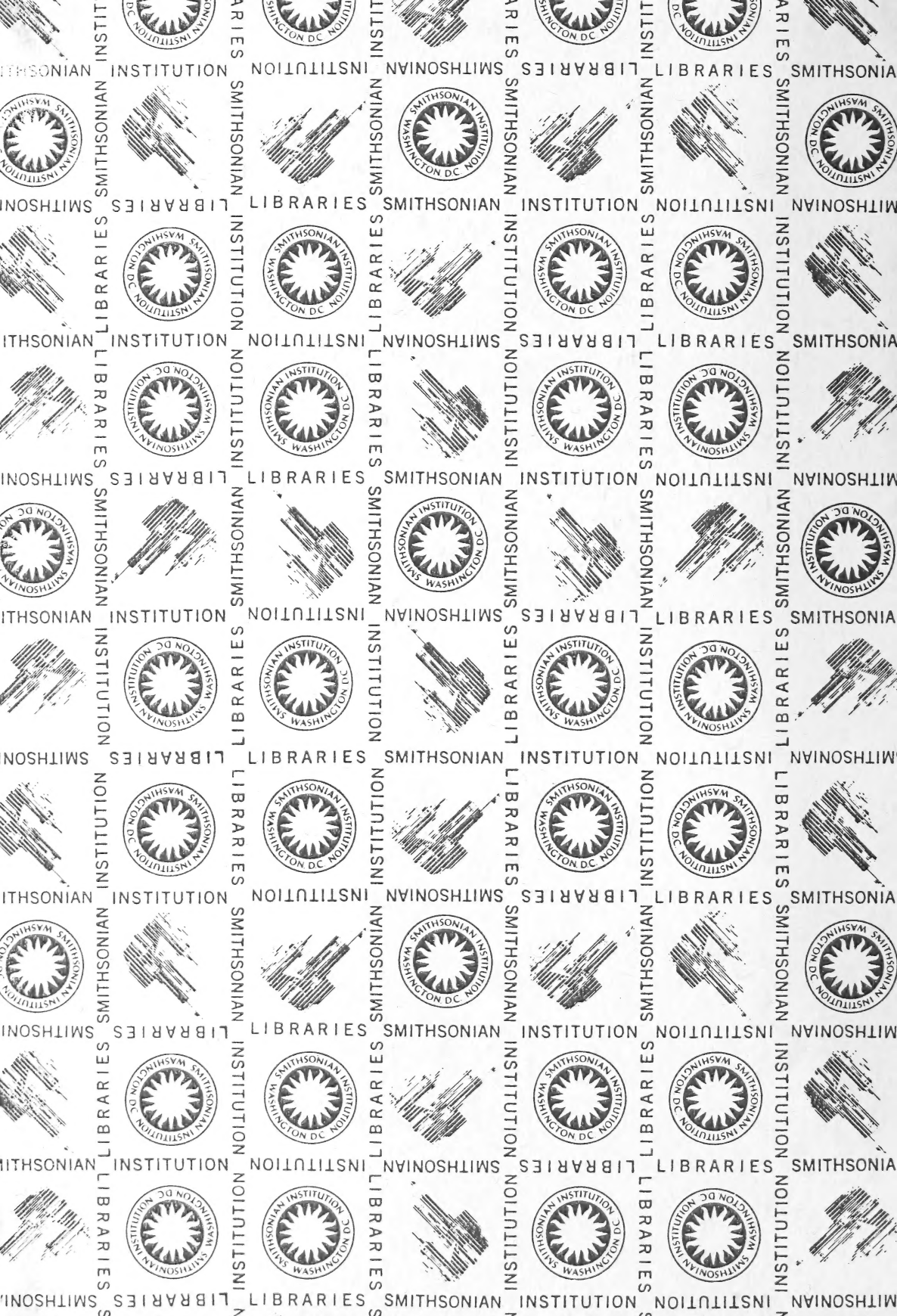
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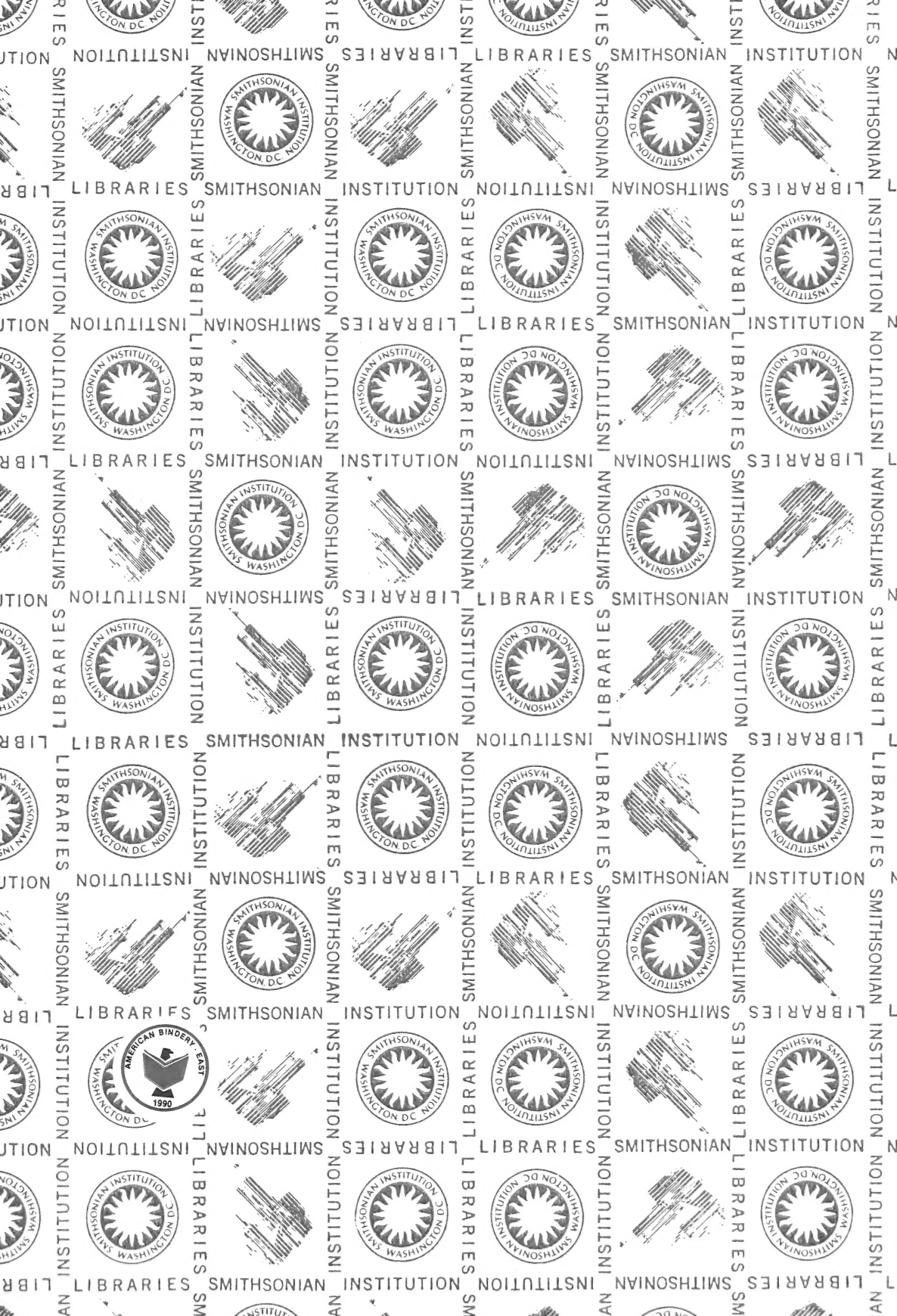
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J. LAURENS BARNARD

THE SYNONYMIZATION OF *TRIODOS*
K. H. BARNARD WITH *AMPELISCA* KRÖYER
(CRUSTACEA, AMPHIPODA)







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